













# SMITHSONIAN

## MISCELLANEOUS COLLECTIONS

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VOL. 144

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"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,  
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—JAMES SMITHSON

(PUBLICATION 4512)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
1962

SMITHSONIAN

MISCELLANEOUS COLLECTIONS

VOL. IV

PORT CITY PRESS, INC.  
BALTIMORE, MD., U. S. A.



THE SMITHSONIAN INSTITUTION  
WASHINGTON, D. C.

1911

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LEONARD CARMICHAEL,  
*Secretary, Smithsonian Institution.*





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2. GREENEWALT, CRAWFORD H. Dimensional relationships for flying animals. 46 pp., 17 figs. Apr. 6, 1962. (Publ. 4477.)
3. KIER, PORTER M. A revision of the cassiduloid echinoids. 262 pp., 44 pls., 184 figs., 7 charts. June 26, 1962. (Publ. 4500.)









SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 144, NO. 1

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Charles D. and Mary Vaux Walcott  
Research Fund

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A FURTHER STUDY OF THE LOWER  
EOCENE MAMMALIAN FAUNAS OF  
SOUTHWESTERN WYOMING

(WITH 14 PLATES)

By

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(PUBLICATION 4474)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
JANUARY 17, 1962



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MAMMALIAN FAUNAS OF SOUTHWESTERN  
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(With 14 Plates)

INTRODUCTION

Continued exploration for the Smithsonian Institution of the early Tertiary deposits of the Wyoming region has included further investigation of the lower Eocene sequence in the southwestern part of the State. Collections described by the author in 1952 were derived principally from the Knight beds along the Green River in the vicinity of La Barge and Big Piney in Sublette County, although scant remains from other localities and horizons were discussed. Particular attention to the less well represented occurrences has since resulted in considerably larger collections furnishing us with much better information on various faunas and their age relationships.

The later work in this area by the author's field party was directed in a large measure toward increasing the faunal representation from the New Fork beds above the Tipton tongue in the northerly part of the Green River Basin. Repeated search with the development of quarries in the lowest levels of the Knight near Bitter Creek Station in the Washakie Basin proved fruitful in adding significantly to the collections made here by Cope in 1872 and by Marsh in 1876 and 1882. Work in the Washakie Basin has also included systematic search of the Cathedral Bluffs beds and of the higher levels of the Knight below the Tipton tongue of the Green River formation in selected areas, particularly in the eastern portion. Moreover, detailed examination was made of widely scattered exposures of the Knight in

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<sup>1</sup> Study of early Tertiary mammals is currently aided by a grant from the National Science Foundation.



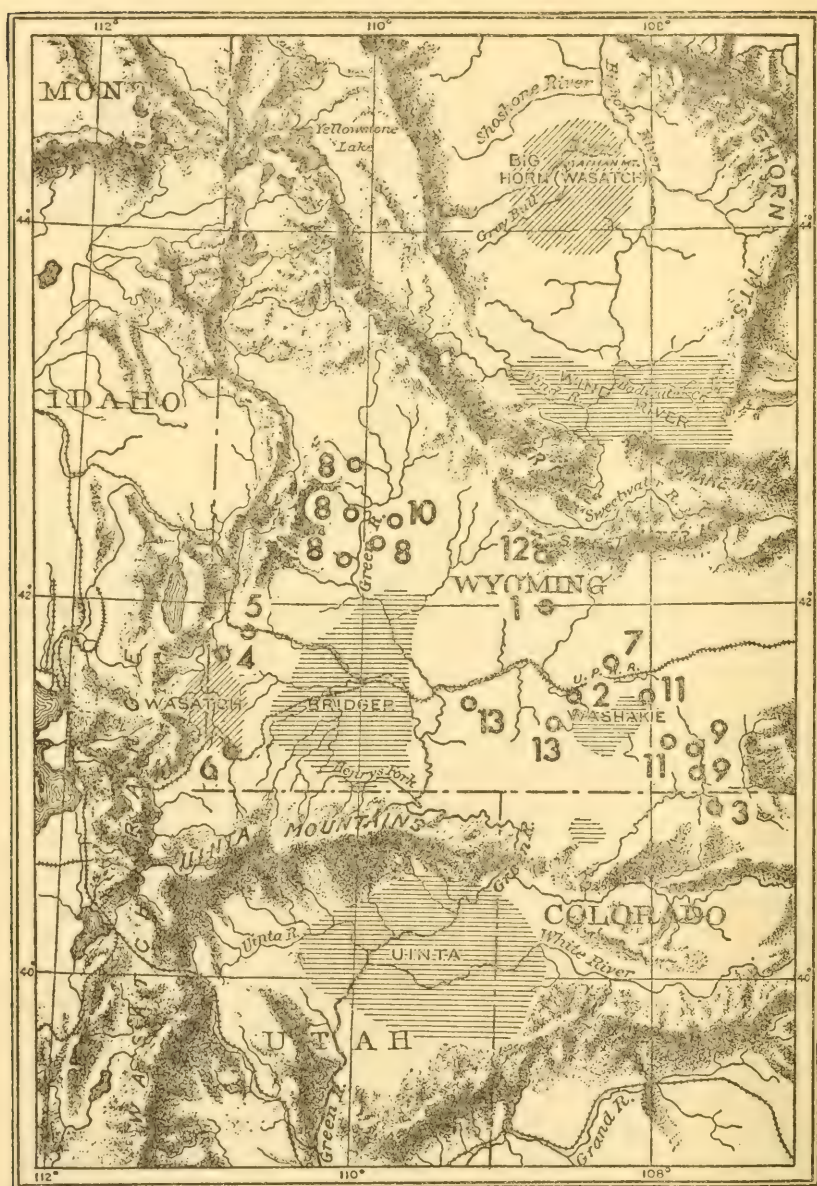


FIG. 1.—Map of southwestern Wyoming and portions of adjacent States showing Eocene basins of deposition, with fossil localities in Wasatch formation numbered as follows: 1, Red Desert; 2, Bitter Creek; 3, Four Mile Creek; 4, W. of Elk Mountain; 5, Fossil Butte; 6, Knight Station; 7, Tipton Butte; 8, La Barge; 9, Dad; 10, New Fork; 11, Cathedral Bluffs; 12, Oregon Buttes; 13, Rock Spring uplift (both flanks). (Map reproduced from Osborn, U. S. Geol. Surv. Monogr. 55, figs. 9, 49, 1929.)

the Fossil Basin, uncovering new localities in the local basin to the west and southwest of Elk Mountain in addition to those previously known around Fossil Butte and in the vicinity of Knight Station. A summary of these investigations was prepared for the 1959 guidebook of the Intermountain Association of Petroleum Geologists for their field conference relative to the Wasatch and Uinta Mountains.

#### ACKNOWLEDGMENTS

Among the many who have been of assistance to me in this restudy of these faunas, I am particularly indebted to the following:

Dr. Joseph T. Gregory, while at Yale University, kindly turned over to me for inclusion in this investigation the interesting collection of unstudied materials made near Bitter Creek by O. C. Marsh's parties. Dr. Peter Robinson supplemented this by sending me from time to time occasional specimens of this collection later encountered during his curatorial work on the Eocene mammals of the Marsh Collection. Dr. Glenn L. Jepsen, in addition to permitting me access to various lower Eocene collections at Princeton University, was most helpful in lending me for review the collections of lower Eocene mammals from the Washakie Basin. The latter were made by Dr. William J. Morris and included specimens representative of both the Dad and Cathedral Bluffs faunas. Dr. Malcolm C. McKenna, while a student at the University of California, sent me for study a collection of teeth that his party made in beds beneath the Tipton tongue near Dad, during the time of their work at the Four Mile Creek locality in nearby Colorado. I was also permitted, through the kindness of Drs. M. Graham Netting and J. LeRoy Kay, to examine the Dad locality materials collected by Kay. These were the specimens reported but not seen by me in 1952. More recently I have been privileged to examine for report several small collections made by Henry W. Roehler of the Mountain Fuel and Supply Co. from a series of carefully documented localities in lower Eocene strata of various horizons on the flanks of the Rock Springs uplift. Dr. Paul O. McGrew of the University of Wyoming has also aided in furnishing me with selected artiodactyl and primate specimens of particular interest that University of Wyoming parties obtained at various localities in the region.

During the faunal study I have been permitted unrestricted access to the type and other comparative materials in the collections of the American Museum, through the courtesy of Drs. George G. Simpson, Edwin H. Colbert, and Bobb Schaeffer. Mrs. Rachel H. Nichols,

former scientific assistant, was particularly helpful in locating specimens and arranging for loan of materials.

As in previous years I was assisted in the field during the more recent investigations of 1953 to 1959 by Franklin L. Pearce, chief of our laboratory of vertebrate paleontology, with the additional help of Theodore B. Ruhoff in 1956. In 1953 George Pipiringos of the U. S. Geological Survey kindly conducted us to various fossil localities that he and Dr. R. W. Brown had located the year before. These included the Red Desert locality east of Steamboat Mountain and sites near Tipton Butte, from which collections had been sent to me for identification and report in 1952, but too late for my paper of that year.

Most important to the value of this study are the incomparable pencil drawings prepared for the accompanying plates by Lawrence B. Isham, staff illustrator for the Department of Geology in the U. S. National Museum.

#### GEOLOGIC RELATIONS

Important new information on the geologic ages and sequence of early Tertiary formations in the southwestern part of Wyoming, particularly in the Fossil Basin and adjacent parts of Utah, necessitates a restatement of geologic relations, modifying the summary and definitions of usage presented in 1952. Much of this relates to demonstration by Tracey and Oriel (1959) that the Fowkes formation is stratigraphically higher than the Knight and a revision by Bradley (1959) of the nomenclature and relationships of members of the Green River formation in the Wyoming area. Further information on ages of various horizons in this sequence likewise calls for additional discussion.

*Evanston formation.*—The earliest formation in the Fossil Basin including strata of Tertiary age is the Evanston. Fossil mammal materials encountered (Gazin, 1956a) near Fossil Station on the Union Pacific Railway demonstrate that the uppermost beds of this unit are Tiffanian Paleocene in age. Tracey and Oriel (1959) found ceratopsian dinosaur materials in the lower part of the formation, showing that beds as old as upper Cretaceous are also included.

*Wasatch formation.*—The original definition of Wasatch by Hayden (1869) can only be interpreted as including the section of essentially reddish or variegated beds extending from near Carter, Wyo., to the "Narrows" of Echo Canyon in Utah. Moreover, Hayden's selection of the term "Wasatch" cannot be interpreted as implying a type sec-





and hence not included within the group of reddish beds that were involved in the original definition of Hayden. Secondly, Veatch considered that the reddish and essentially conglomeratic beds in Echo Canyon correlated with his Almy. Much of the sequence exposed in Echo Canyon is unconformably beneath the Tertiary, and in a recent paper by Williams and Madsen (1959) the older beds have been named the Echo Canyon conglomerate. They report fossils identified by Cobban as demonstrating a Cretaceous age, possibly late Niobrara. These exposures, it may be recalled, are those most glowingly described by Hayden, and are as much a part of the original Wasatch as is the Knight. This is, of course, an unwarranted extension of the group concept.

The U. S. Geological Survey and others have often extended use of "Wasatch" to designate reddish or variegated beds in many remote areas and basins not a part of the basin of deposition for which Wasatch was originally proposed. This practice is, of course, unacceptable by standards based on probable formation continuity, and by such designation the geologist can only be implying a color resemblance, or more often than not he is using it as a time term to indicate an early Eocene(?) age.

The term "Wasatch" no doubt should be abandoned but it has become so deeply entrenched in the literature that this may not be feasible. Redefinition to exclude the Echo Canyon conglomerate would, in general, conform to later usage in southwestern Wyoming. This would involve beds that have been described by Veatch as Almy and Knight in the Fossil Basin, but exclude, of course, the Evanston formation. The Almy is nearly unfossiliferous in the type area and although it appears to occupy a position stratigraphically between the Evanston and Knight, suggesting an uppermost Paleocene or Clarkforkian age, it is regarded by Tracey and Oriel (oral communication) as probably no more than a coarser or marginal facies of the Knight.<sup>2</sup> Wasatch in this manner is restricted to scarcely more than formation significance in the Fossil Basin, and probably also in the adjacent part of Utah.

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<sup>2</sup> During the 1961 field season, after this paper had gone to press, determinable remains of fossil mammals were encountered by Franklin L. Pearce, Steven S. Oriel, and myself in beds mapped by Veatch as Almy on the north side of Red Canyon just to the east of the town of Almy. Several genera are recognized and an early Eocene age is evident, demonstrating that the "Almy" in its typical area is a coarser facies of the Knight. Details of the occurrence, the fauna represented and conclusions to be drawn are being prepared as a separate geological note by Tracey, Oriel, and myself.

The foregoing, together with a recent decision (Feb. 24, 1960) of the Geologic Names Committee of the U. S. Geological Survey to recognize "Wasatch formation" in preference to "Knight formation" for the concerned beds in southwestern Wyoming, has led me to revise usage in this paper from that adopted in my 1952 and 1959 reports on the faunas, complying to this extent with nomenclature henceforth to be used by the U. S. Geological Survey. The term Knight, however, I have retained in this study to designate a member of the Wasatch formation. It is restricted from my earlier usage in the Green River and Washakie Basins to include only the lower Eocene portion of the Wasatch that is beneath the Tipton tongue (see fig. 2), excluding the Cathedral Bluffs tongue of the Wasatch and its equivalent New Fork tongue.

The type section of the Knight, as defined by Veatch, is in the Fossil Basin; and the unit in this general area has been demonstrated to include beds from lowest Eocene to at least as high as Lysite, but whether or not strata of Lost Cabin equivalence are present has not been shown. The sequence does involve these later beds in the Green River and Washakie Basins and hence does not appear to be entirely equivalent. Nevertheless, the two sequences are essentially continuous to the east of Evanston and there would seem to be no logical reason for separate designation in any of the complex of adjoining basins having contiguous early Eocene deposition in the southwestern part of the State.

*Wasatchian*.—Although recognizing the term "Wasatch" to be variously misused and adopting it only as a group term, the Society of Vertebrate Paleontology's committee on Nomenclature and Correlation of the North American Continental Tertiary in 1941 (Wood, et al.) proposed and defined the term "Wasatchian" as an arbitrary time or age designation to include the lower part of the Eocene, older than Bridgerian or middle Eocene. The term "Wasatchian" is clearly limited by definition to the Eocene and is not intended to include the Paleocene portion of time that seems evident for earlier strata that might be included in the Wasatch formation.

*Green River formation*.—W. H. Bradley in 1959 revised the stratigraphic nomenclature of the Green River formation in Wyoming. Recognizing that the "Laney" of the Bridger Basin interfingered with the Cathedral Bluffs tongue northeast of White Mountain and was hence stratigraphically older than the type Laney in the Washakie Basin which overlies the type Cathedral Bluffs, he gave the new name "Wilkins Peak" member to the "Laney" of the Bridger Basin. At



the same time he concluded that his Morrow Creek member, which overlies the Wilkins Peak, must then be equivalent to the type Laney and should therefore be abandoned.

From this it is seen that in the Bridger or Green River Basin the New Fork tongue, which is evidently equivalent to the Cathedral Bluffs tongue, overlies the Fontenelle or Tipton tongue, interfingers with the Wilkins Peak and is overlain by the Laney member of the Green River. Evidently the Wilkins Peak member is present only in the Bridger Basin, so that to the east of the Rock Springs uplift the widespread Cathedral Bluffs tongue overlies the Tipton tongue and is overlain by the Laney member.

#### THE MAMMALIAN FAUNAS

The various Mammalia encountered at the several general localities and horizons in the lower Eocene beds of southwestern Wyoming are included together in the following composite list and checked to show representation in the more important localities for these horizons.

#### OCCURRENCES AND FAUNAL CORRELATIONS

The various collecting localities included in the apposing list, for the most part rather general areas representing subdivisions of Wasatchian time, are discussed in following sections. To these, however, are added consideration of the Four Mile Creek localities in Colorado that were studied by Malcolm C. McKenna, the series of localities in stratigraphic sequence on the flanks of the Rock Springs uplift that were systematically developed by Henry W. Roehler, and a few occurrences of lesser faunal importance that seem worthy of mention.

*Red Desert.*—The locality referred to as Red Desert in the attendant check list is a small area of buff, coarse-grained sandstone which outcrops in about sec. 12, T. 23 N., R. 100 W., approximately 14 miles east of Steamboat Mountain to the north of the Rock Springs uplift. The horizon here represented is near the base of Pipiringos's Red Desert tongue and judged by him to be about 200 feet above the Eocene-Paleocene contact. The small patch of sandstone shows much evidence of wind erosion, and the rather fragmentary materials obtained, consisting mostly of isolated teeth, would appear to be a part of a residual concentration of coarser particles left by the wind.

The fauna represented includes such characteristic Wasatchian forms as *Pelycodus*, *Esthonyx*, *Phenacodus*, *Hyracotherium*, and *Diacodexis* but evidence for an early Gray Bull equivalence is seen in the condylarth *Haplomylus speirianus*. A correspondence to the Four

[illegible]

	Red Desert	Bitter Creek	W. of Elk Mt.	Fossil Butte	Knight Station	La Barge	Dad	New Fork	Cathedral Bluffs
<b>Taeniodonta:</b>									
<i>Ectoganus</i> , sp. ....	..	..	..	X	..	..	..	..	..
Undetermined stylinodont .....	..	..	..	..	..	X	..	..	..
<b>Edentata:</b>									
<i>Pentapassalus pearcei</i> Gazin.....	..	..	..	..	..	X	..	..	..
<b>Rodentia:</b>									
<i>Paramys excavatus</i> Loomis.....	..	X	X	..	X	X	..	..	..
<i>Paramys copei</i> Loomis.....	..	..	..	..	..	X	X	..	X
<i>Paramys major</i> Loomis.....	..	..	..	..	..	X	X	X	X
<i>Reithroparamys</i> , sp. ....	..	..	..	X	..	..	..	..	..
<i>Microparamys</i> , sp. ....	..	..	..	..	..	..	..	..	X
<i>Knightomys senior</i> (Gazin).....	..	..	..	..	..	X	..	..	..
<i>Dawsonomys woodi</i> Gazin.....	..	..	..	..	..	X	..	..	..
<i>Sciuravus wilsoni</i> Gazin.....	..	..	..	..	..	..	..	X	X
<b>Carnivora:</b>									
<i>Thryptacodon</i> , near <i>T. antiquus</i>									
Matthew .....	..	..	..	..	..	X	..	..	..
<i>Hapalodectes compressus</i> Matthew..	..	..	..	..	..	..	..	X	..
<i>Pachyaena ossifraga</i> Cope.....	..	X	..	..	..	..	..	..	..
<i>Pachyaena gracilis</i> Matthew.....	..	..	X	?	..	..	..	..	..
<i>Pachyaena?</i> , sp. ....	..	..	..	..	..	..	..	X	..
<i>Oxyaena</i> sp. ....	..	X	..	..	..	X	X	..	..
<i>Ambloctonus major</i> Denison.....	..	..	..	..	..	X	X	..	..
<i>Prolimmocyon elisabethae</i> Gazin.....	..	..	..	..	..	X	..	..	..
<i>Prolimmocyon</i> , cf. <i>antiquus</i> Matthew.	..	..	..	..	..	..	..	X	..
<i>Sinopa</i> , near <i>S. viverrina</i> (Cope)...	..	..	..	..	..	X	..	..	..
<i>Sinopa</i> , cf. <i>multicuspis</i> (Cope).....	..	X	X	X	..	..	..	..	..
<i>Sinopa</i> , cf. <i>vulpecula</i> Matthew.....	..	..	..	..	..	X	..	X	..
<i>Sinopa</i> , cf. <i>strenua</i> (Cope).....	..	..	X	..	..	X	..	..	..
<i>Didymictis protenus</i> (Cope).....	..	X	X	..	..	..	?	..	..
<i>Didymictis altidens</i> Cope.....	..	..	..	X	..	X	..	X	X
<i>Viverravus</i> , cf. <i>acutus</i> Matthew.....	..	X	..	..	..	..	X	..	..
<i>Viverravus lutosus</i> Gazin.....	..	..	..	..	..	X	..	X	X
<i>Viverravus</i> , cf. <i>dawkinsianus</i>									
(Cope) .....	..	..	..	..	..	..	..	X	..
<i>Umtacyon asodes</i> Gazin.....	..	..	..	..	..	X	..	X	..
<i>Miacis</i> , near <i>M. exiguus</i> Matthew...	..	..	..	..	..	X	..	X	..
<i>Miacis</i> , cf. <i>latidens</i> Matthew.....	..	..	..	..	..	X	..	..	..
Cf. <i>Vulpavus australis</i> Matthew.....	..	..	..	X	..	..	..	..	..
<i>Vulpavus asiaticus</i> Gazin.....	..	..	..	..	..	X	X	X	..
Cf. <i>Vulpavus</i> , sp.....	..	X	..	..	..	..	..	..	..
<i>Vassacyon</i> , cf. <i>promicrodon</i>									
(Wortman) .....	..	..	X	..	..	..	..	..	..

	Red Desert	Bitter Creek	W. of Elk Mt.	Fossil Butte	Knight Station	La Barge	Dad	New Fork	Cathedral Bluffs
<b>Condylarthra:</b>									
<i>Haplomylus speirianus</i> (Cope).....	X	X	X	..	..	..	..	..	..
<i>Hyopsodus loomisi</i> McKenna.....	X	X	..	..	..	..	..	..	..
<i>Hyopsodus</i> cf. <i>miticulus</i> (Cope)...	..	X	X	X	..	..	..	..	..
<i>Hyopsodus wortmani</i> Osborn.....	..	..	..	..	..	X	X	X	..
<i>Hyopsodus</i> , cf. <i>mentalis</i> (Cope)....	..	..	..	..	..	X	..	X	..
<i>Hyopsodus browni</i> Loomis.....	..	..	..	X	X	..	X	..	X
<i>Hyopsodus</i> , cf. <i>walcottianus</i>									
Matthew .....	..	..	..	..	..	..	X	X	..
<i>Phenacodus</i> , cf. <i>primaevus</i> Cope.....	..	X	..	..	X	..	..	..	..
<i>Phenacodus</i> , cf. <i>wortmani</i> (Cope)...	..	..	X	..	..	..	..	..	..
<i>Phenacodus</i> , cf. <i>brachypternus</i> Cope.	X	..	..	..	..	..	..	..	..
<i>Meniscotherium</i> , cf. <i>priscum</i>									
Granger .....	X	X	..	..	..	..	..	..	..
<i>Meniscotherium robustum</i> Thorpe...	..	..	?	?	..	X	..	..	..
<i>Meniscotherium</i> , cf. <i>chamense</i> Cope..	..	..	..	..	..	..	..	X	..
<b>Pantodonta:</b>									
<i>Coryphodon radians</i> (Cope).....	..	X	X	X	X	X	X	..	..
<b>Dinocerata:</b>									
Cf. <i>Bathyopsis fissidens</i> Cope.....	..	..	..	..	..	..	..	X	..
<b>Perissodactyla:</b>									
<i>Hyracotherium</i> , cf. <i>angustidens</i>									
(Cope) .....	X	X	X	..	..	..	..	..	..
<i>Hyracotherium vasaccense</i> (Cope)...	..	..	..	X	X	X	X	X	X
<i>Hyracotherium</i> , cf. <i>craspedotum</i>									
Cope .....	..	..	..	X	..	X	X	X	X
<i>Lambdaotherium popoagicum</i> Cope...	..	..	..	..	..	X	X	X	..
Brontotheriid, near <i>Palaeosyops</i>									
<i>fontinalis</i> Cope .....	..	..	..	..	..	..	..	..	X
<i>Homogalax primaevus</i> (Wortman)...	..	X	..	..	..	..	..	..	..
Isectolophid, near <i>Homogalax</i>									
<i>primaevus</i> (Wortman)) .....	..	..	..	..	..	..	X	..	..
<i>Heptodon ventorum</i> (Cope).....	..	..	..	X	X	X	X	X	..
<i>Hyrachyus</i> , cf. <i>modestus</i> (Leidy)....	..	..	..	..	..	..	..	X	X
<b>Artiodactyla:</b>									
<i>Diacodexis</i> , cf. <i>metsiacus</i> (Cope)...	X	X	X	..	..	..	..	..	..
<i>Diacodexis</i> , near <i>D. secans</i> (Cope)...	..	..	..	..	..	X	?	X	..
<i>Diacodexis</i> , cf. <i>robustus</i> Sinclair....	..	..	..	..	..	..	X	..	..
<i>Bumophorus</i> cf. <i>macropternus</i>									
(Cope). .....	..	..	..	..	..	X	X	..	..
<i>Bumophorus</i> , cf. <i>etsagicus</i> (Cope)...	..	..	..	..	..	..	..	X	..
<i>Hexacodus pelodes</i> Gazin.....	..	..	..	..	X	X	X	X	X
<i>Hexacodus uintensis</i> Gazin.....	..	..	..	X	X	..	..	..	..



Mile fauna described by McKenna is suggested by an upper molar referred to primitive *Hyopsodus loonisi*, and by this together with a lower molar of *Pelycodus* (?) *praetutus* and teeth of *Meniscotherium*, cf. *priscum*, a resemblance to the Bitter Creek fauna is also seen.

*Bitter Creek*.—Most significant of the newly worked localities is a prominent hill of north- and westerly-facing exposures approximately a mile and a quarter south of Bitter Creek Station on the Union Pacific Railroad in Sweetwater County. This is surely the locality Cope (1872) referred to as Black Buttes in his description of *Coryphodon armatus*. It is the nearest exposure of Wasatchian materials to the Black Buttes station a few miles to the west, and the topographic feature of that name is still more remote in the older formations of the Rock Springs uplift. Marsh's parties also made collections here in 1876 and 1882, including the specimens he described as *Eohippus pernix*. The Marsh material, except for the hyracothere, has not been previously described. The exposures at this locality are on the west or northwest side of the Washakie Basin and may likewise be considered as on the east flank of the Rock Springs uplift. The locality is in the lowest part of the Knight, but little above the Paleocene. The contact or transition between these sets of beds is obscured locally by the alluvium of Bitter Creek. Fossils were encountered in various lithologic zones, including the thicker sandy marls, where more than one good skull of *Coryphodon* was obtained, but many of the smaller jaws and teeth were found in or adjacent to the thin carbonaceous layers which abound in spines and other fragments of fish.

A fauna of about 24 species of mammals representing 21 genera was recognized in the combined National Museum and Yale University collections. The fauna closely resembles that of the Gray Bull beds in the Bighorn Basin, and the small condylarths *Haplomylus speirianus* and *Meniscotherium*, cf. *priscum*, suggest correlation with the earlier part of Gray Bull series. The genera here are nearly all included in the larger Four Mile fauna and differences in certain of the species represented may in part reflect local conditions or environment. Most noticeable with regard to the Four Mile fauna is the absence of *Meniscotherium*, which so far has not been found in any of the horizons on the east side of the Washakie Basin. This must surely represent a persistent ecological difference.

*Four Mile Creek*.—To the southeast of the Washakie Basin in the adjacent part of Colorado, but nevertheless within the more general area of the Washakie basin of deposition, a number of localities in

exposures very low in the Knight have yielded remains of a fauna of considerable size. Collecting here was done by University of California parties and the collections, made largely by a washing technique, were described in detail by McKenna (1960). The localities from which these materials were obtained are shown in a map accompanying his report.

The Four Mile fauna is equivalent in age to the early part of the Gray Bull beds, or essentially the Sand Coulee level, in the Bighorn Basin. These collections have not been examined by me, and no direct comparison of the materials with, for example, those from Bitter Creek has been made, so that a comparative listing here seemed inadvisable.

*West of Elk Mountain.*—Exploration of the Knight was extended to include a variety of localities in the Fossil Basin along the western margin of the State in Lincoln and Uinta Counties. Newly discovered localities in the valley of North Bridger Creek to the west of Elk Mountain, however, while only sparsely fossiliferous, have produced as representative a collection as that obtained at Fossil Butte. The localities are low on a west-facing escarpment that is capped with Green River beds west and southwest of Elk Mountain. The occurrences are scattered along exposures due west of Elk Mountain, where remains were found near the base of the sequence, to about three or four miles farther south, in or near sec. 30, T. 20 N., R. 119 W., where collecting was done at a somewhat higher level. In this area, as near Fossil Station, the Knight is resting directly on the Evanston formation.

About 13 genera of mammals are recognized and remains of one species, *Haplomylus speirianus*, suggesting early Gray Bull although not necessarily Sand Coulee, were found at the locality near the base of the section due west of Elk Mountain. *Vassacyon*, cf. *promicrodon*, found a couple of miles farther south near a specimen of *Phenacodus*, cf. *vortmani*, may also be indicative of Gray Bull time, but not necessarily the earliest part. Although the remaining forms for the most part do not seem to be critical as to horizon, they are, except for a recently discovered specimen of *Meniscotherium*, cf. *robustum*, forms to be expected in levels of Gray Bull equivalence. It may be further noted that *Coryphodon* is more than usually abundant along the lower slopes of the escarpment and some rather good skull and jaw material was obtained.

*Fossil Butte.*—Fossil Butte derives its name from the well-known fossil fish quarries in the Green River formation that caps this butte



and nearby ridges in the vicinity of Fossil Station on the Oregon Short Line branch of the Union Pacific Railroad. A number of specimens of fossil mammals have been found in the variegated Knight beds beneath the Green River beds around Fossil Butte and adjacent areas. It is here that specimens first found by Princeton University parties in 1939 and 1940 were reported by me in 1952. Smithsonian Institution parties obtained a number of specimens from west-facing exposures in the saddle to the north of Fossil Butte as well as on the more accessible slopes around the south side of the butte.

I am not certain that the remains collected on the slopes of Fossil Butte all represent the same division of Wasatchian time. *Heptodon* has been found only high on the slopes in the somewhat darker red beds close beneath the Green River shales. Also, the tooth portions of *Didymictis* considered to represent *D. altidens* were from a high level. It is clear that these upper slopes are later than Gray Bull and the presence there of *Hyopsodus browni* would suggest Lysite—but finding this species or a form within the same size range in the Dad fauna, in association with *Lambdaotherium*, somewhat weakens this particular evidence. The absence of *Meniscotherium*, so abundant in the nearby La Barge localities, had been thought significant but the more recent finding of a maxilla in the saddle to the north of Fossil Butte and a lower jaw portion on the east side would appear to rule out this evidence also; however, the species represented may not be typical *M. robustum* because of the comparatively small size of the teeth. Nevertheless, the absence of *Lambdaotherium*, invariably found in beds just below the Tipton tongue of the Green River beds belonging to Lake Gosiute, lends tentative support to a Lysitean age assignment. The remaining forms represented on the higher slopes of the butte, i.e., *Pelycodus*, near *P. jarrovii*; *Ectoganus*, sp.; *Reithroparamys* sp.; *Sinopa*, cf. *multicuspis*; cf. *Vulpavus australis*; *Hyopsodus*, cf. *miticulus*; *Hyracotherium*; and *Hexacodus nintensis* apparently do not furnish critical information. It may be further noted, however, that the species of *Hexacodus* cited is not the same as that in the La Barge fauna.

While there does not appear to be any certain evidence to demonstrate that the lower part of Fossil Butte is older than Lysite, it should be noted that *Coryphodon* seems much more abundant on the middle and lower slopes, much as it is to the west of Elk Mountain and at Bitter Creek. In addition to *Coryphodon*, sp.; *Diacodon*, cf. *alticuspis*; *Pelycodus*, near *P. jarrovii*; cf. *Pachyaena gracilis*;

*Hyracotherium*, sp.; and *Hexacodus uintensis* have been found at the lower levels.

*Knight Station*.—The localities along Bear River to the southeast of Evanston and in the vicinity of Knight Station were discussed in 1952 and further exploration by Smithsonian Institution parties has failed to uncover additional materials of new significance. Granger (1914, p. 203) regarded these beds as equivalent to Lysite in age and to date I find no reason to question seriously this conclusion. Among the forms now recognized in the fauna from this locality there may be listed the following:

<i>Cynodontomys</i> , sp.	<i>Coryphodon radians</i> (Cope) (etc.)
<i>Esthonyx</i> , sp.	<i>Hyracotherium vasaccense</i> (Cope)
<i>Paramys excavatus</i> Loomis	(incl. <i>H. index</i> )
<i>Hyopsodus browni</i> Loomis	<i>Heptodon ventorum</i> (Cope)
<i>Phenacodus primaevus</i> Cope	<i>Hexacodus pelodes</i> Gazin
	<i>Hexacodus uintensis</i> Gazin

Granger's conclusions were based on the presence of *Heptodon*, which distinguished these beds from the Gray Bull level, and on the species of *Cynodontomys* and *Hyopsodus* which he regarded as nearest to Lysite forms of these genera. The *Cynodontomys* specimen may well represent *C. latidens* but the absence of premolars leaves much to be desired. The *Hyopsodus* is of a size that strongly suggests Lysite *H. browni*, but there is recent evidence to indicate that a form of this size is present in the Dad fauna. Elsewhere this has not been found in the La Barge horizon. The two species of *Hexacodus* listed are based on the specimens listed by Van Houten (1945, p. 458) from American Museum labels as *Diacodexis*, sp. These had not been seen at the time of the 1952 report but have since been found and their identity is discussed under the species of *Hexacodus*.

Identifiable remains of mammals are not frequently encountered in the type section of the Knight, but of those found *Coryphodon* seems most conspicuous, with *Heptodon* and *Hyracotherium* represented by remains from more than one individual. The absence of *Lambdotherium*, while entirely inconclusive, permits retention of a Lysite assignment.

*Tipton Butte*.—A locality near Tipton Butte that has produced a number of isolated teeth was found by Roland W. Brown and George N. Pipiringos in 1952. It is in the SW $\frac{1}{4}$  sec. 23, T. 20 N., R. 96 W., near the top of the Red Desert member described by Pipiringos (1955, p. 100). Recognized among the teeth are a small form of *Cynodontomys* that may be *C. angustidens*; *Pelycodus*?, sp.; *Es-*

*thonyx bisulcatus*; *Paramys*, cf. *excavatus*; *Vulpavus*, possibly *V. asius*; *Hyopsodus*, sp.; *Meniscotherium* cf. *robustum*; and *Hyracotherium*. I earlier reported these to Pipiringos as being about equivalent to Lysite or Lost Cabin in age. I believe now, however, that the age is probably not as late as Lost Cabin. It may well be Lysitian or late Graybullian, but the evidence is not critical.

*La Barge*.—The outstanding occurrence or series of localities in the Knight member is that for the La Barge fauna in the vicinity of La Barge and Big Piney, essentially all in Sublette County. As described in 1952, the horizon of the Knight involved is exposed principally in the various canyons or draws on both sides of the Green River between La Barge and Big Piney and to a point about 12 miles north of Big Piney. Fossil remains were encountered from a few feet to more than a hundred feet below the Tipton (Fontenelle of Donovan) tongue of the Green River. Certain of the more profitable localities in these beds have been revisited on various occasions in later years, particularly that on Muddy Creek near where it is crossed by the highway north from Big Piney.

Most of the 1952 report was devoted to the La Barge fauna, and the evidence relating to its Lostcabinian age considered in detail (1952, pp. 10-12). The significance of the occurrence of the species *Meniscotherium robustum* discussed then has since been modified by various scattered finds in the northern part of the Fossil Basin, and new information on the fauna is afforded by recognition in it of such genera as *Palaeictops*, *Apatemys*, *Omomys*, *Chlororhysis*, *Knightomys*, and *Dawsonomys* not cited in the earlier list. The number of genera of mammals now identified in the fauna is 31, representing about 40 species, out of an entire number of about 53 genera and approximately 95 species considered in this report for the lower Eocene portion of the Wasatch. This total number does not include early Knight occurrences in Colorado described by McKenna.

*Dad*.—A long escarpment of Knight exposures beneath the Tipton tongue on the east side of the Washakie Basin, well known to collectors in the Wyoming region, extends along the west side of Muddy Creek and highway U.S. 330 from near Dad P. O. southward, interrupted by several long canyons heading to the west, to the vicinity of Baggs. While specimens have been found in many scattered localities, most of the material collected by the Smithsonian Institution, Carnegie Museum, and University of California parties has been from the large promontory-like exposures near Dad. *Hyracotherium* is particularly common in this area.



The stratigraphic position of the occurrences referred to as the Dad locality appears similar to that for the La Barge area relative to the Tipton tongue, and the faunas represented are similar in the identity of several species. Among those in common may be mentioned *Chlororhysis knightensis*, *Paramys copei*, *Paramys major*, *Ambloctonus major*, *Vulpavus asiaticus*, *Hyopsodus wortmani*, *Coryphodon*, cf. *radians*, *Hyracotherium vasaccense*, *Hyracotherium*, cf. *craspedotum*, *Lambdotherium popoagicum*, and *Heptodon ventorum*. Several of these are not particularly significant as to the horizon of the Knight represented but the occurrence of *Lambdotherium* would seem to limit it to Lostcabinian time. There are, nevertheless, a number of differences that are noteworthy, but which can possibly be attributed to local environment or ecology. The absence of *Meniscotherium*, so abundant in the La Barge fauna—missing from all horizons on the east side of the Washakie Basin—must surely be related to ecology. Not so easily explained perhaps are certain forms that seem rather primitive for this level, such as indicated by the materials that have been tentatively referred to *Didymictis protenus* and *Viverravus acutus*, and the small tooth referred to *Esihonyx*. Moreover, a *Hyopsodus* the size of Lysite *H. browni* is not represented in the rather numerous remains of this genus at La Barge. Particularly surprising is the discovery of isctolophid remains closely resembling *Homogalax*. Too much stress, however, should not be placed on this because of the recognized survival of the isctolophid line into still later Eocene time. The possibility that the lowest exposures along the base of the Baggs-Dad escarpment, where it reaches its greatest height, may include beds older than Lost Cabin should not be disregarded, but unless faulting is involved, surely beds of Gray Bull age would not be exposed so near the Tipton tongue.

*New Fork.*—Of especial importance are the New Fork or Cathedral Bluffs exposures along Alkali Creek in the same general area as those for the La Barge fauna but somewhat farther east of the Green River. Alkali Creek, a dry stream bed most of the year, is roughly parallel to the Green River, descending northward to where it joins the Green River near its confluence with the New Fork. Exposures of the New Fork beds are typically developed along the south side of the New Fork to the east of Big Piney, and on both sides of Alkali Creek. The most productive localities were found to be the series of buttes on the west side of Alkali Creek from its mouth southward for a few miles, beyond which the fluvial series

above the Tipton tongue is replaced by interfingering lake deposits belonging to the Wilkins Peak member of the Green River formation.

Since the preliminary statement on this fauna in 1952, 15 genera have been added to the 10 (one of these, *Ambloctonus*, was cited in error) then recognized. These represent the smaller mammals such as insectivores, primates, rodents, artiodactyls, and particularly carnivores, as may be seen in the foregoing list. The fauna is rather closely related to that of the La Barge horizon, and about 16 species survived without change of significance or taxonomic importance the interval of lake encroachment during which the Tipton tongue was formed. Certain species, however, may be regarded as having evolved more appreciably; suggested are those representing *Cynodontomys*, *Notharctus*, *Prolimmocyon*, and *Bunophorus*. The ecologic changes that accompanied the lake advance no doubt permitted or are responsible for a certain faunal readjustment, with migrations and certain extinctions evident in the local scene, but because of the climatic factor involved this may have been rather widespread. Notable is the disappearance of *Coryphodon*, possibly also of *Thryp-tacodon* and *Ambloctonus*, although these are never common and could have escaped collection in the New Fork. A number of small mammals are not recorded later but their marked scarcity or unique representation precludes any generalizations. Newly introduced into the area are such forms as *Hapalodectes*, *Bathyopsis*, and *Hyrachyus*. *Meniscotherium robustum* evidently became extinct and was replaced from elsewhere by a form that would appear to be *M. chamense*. A new animal to the Green River Basin in New Fork time may also be *Hyopsodus walcottianus*.

*Cathedral Bluffs*.—Above the Tipton tongue in the Washakie Basin the Cathedral Bluffs member has been found to be comparatively barren. Exploration by Smithsonian Institution parties has extended from the northwest around the northern and eastern sides of the basin to near the southeastward limit of the exposures, with the finding of but very occasional scattered specimens. Nevertheless, collecting by William Morris for Princeton University has resulted in representation of a fauna of respectable size. Most of the Princeton material from the Cathedral Bluffs is from the zone of outcrop on the northeast side of the basin, as shown on the map accompanying his report (1954).

About 15 genera are now recognized in this fauna, and though the number is not significantly greater than listed by Morris, there have been some changes in the names applied with a different interpreta-

tion of relationships (see Gazin, 1959, p. 135). All of these are discussed in the systematic portion of this paper, as listed in the preceding section. Of these, all but *Peratherium*, *Trogosus*?, *Ab-sarokius*, *Microparamys*, and the brontotheriid near *P. fontinalis* are represented in the New Fork fauna. Only *Trogosus*? and the brontotheriid appear significant in this difference.

I have earlier (1959) discussed the possibility of the Cathedral Bluffs including upwards beds somewhat later than are represented in the New Fork, particularly to the north of the Washakie Basin in the region of the Oregon Buttes and Cyclone Rim. Although this in no way disturbs the probable contemporaneity of the two sets of beds, at least so far as their relation with the Tipton tongue is concerned, it may be noted that New Fork sequence as exposed in the type area is scarcely more than a remnant near its basinward periphery, where it interfingers with the Wilkins Peak. Most of its faunal remains were recovered in the lower part, no great distance above the Tipton (Fontenelle) tongue, except for *Bathyopsis*, which was discovered several miles farther south on Alkali Creek and possibly a little higher in the section.

Investigation, furthermore, of the particular field occurrences of *Trogosus*?, sp., and the brontotheriid, near *Palaeosyops*? *fontinalis* (earlier listed as *Eotitanops*, sp.), discloses that both were found in sec. 4, T. 15 N., R. 93 W. This is evidently locality 1 on Morris's map (1954, p. 198) and clearly high in the section, as it is near the contact with the overlying Laney shale. Both also have been found in beds mapped as belonging to the Cathedral Bluffs tongue in the Continental Divide Basin farther to the north. The *Trogosus* occurrence reported by Nace (1939, pp. 17, 26-27) was described as occurring 75 feet below the top of the Cathedral Bluffs tongue in the northwest part of T. 26 N., R. 98 W. The brontotheriid near *Palaeosyops*? *fontinalis* was found by me very near the top of the red beds in the Oregon Buttes area, immediately to the southwest of the Continental Peak at the north margin of Sweetwater County. The significance of the brontotheriid occurrences is discussed in the systematic section of this paper. The implication that a "Bridger A" level is represented is probably meaningless. The *Palaeosyops*? *fontinalis* type may well have been found in a sandy lens of the Wilkins Peak member. Robinson (MS.) has shown that the Huerfano B fauna, which includes *Palaeosyops*? *fontinalis*, is associated with a Lost Cabin fauna rather than one truly Bridgerian.

It is now evident that *Trogosus* was not actually in association with



*Esthonyx* in the Cathedral Bluffs, but the gap between them in their stages of development seems too great for direct continuity in the time permitted. *Palaeosyops? fontinalis*, on the other hand, is scarcely more than a large *Eotitanops*.

*Oregon Buttes*.—In addition to the brontotheriid, near *Palaeosyops? fontinalis*, and *Trogosus* discussed in the above section on the Cathedral Bluffs, remains of *Notharctus*, *Hyrachyus*, and a tapiroid which has been thought to represent *Heptodon* have been found in the northwestern part of the Continental Divide Basin, in the general area of the Oregon Buttes and Continental Peak. The Cathedral Bluffs sequence here beneath the lacustrial zone which was mapped as "Morrow Creek" (now Laney) consists essentially of a lower red zone and an upper greenish portion. Part of the specimens collected by us came from a level at about the color change to a few feet higher, but the tapiroid and *Notharctus* came from red beds on the northwest side of Oregon Buttes. These few specimens give no clue as to whether the age represented is that of the Lost Cabin or Bridger beds. The brontotheriid is a trifle more robust than that represented by the Princeton specimen from the Washakie basin, and the *Heptodon*-like tapiroid could be *Heleletes*. The possibility that the color change here represents the transition from Cathedral Bluffs to Bridger makes interesting speculation, particularly since the overlying Laney is so attenuated. It should be noted, however, that much of the New Fork sequence of undoubted Wasatchian age is essentially greenish with locally reddish zones or lenses.

*Rock Springs uplift*.—In 1952 I reported the discovery by Roland W. Brown of *Meniscotherium robustum* and *Coryphodon* in the Knight a few miles southwest of Rock Springs. Since then Henry W. Roehler, geologist for the Mountain Fuel and Supply Co. in Rock Springs, has discovered a series of small faunules at various horizons in the "Hiawatha" member on the west flank of the uplift near here. These included representation of horizons from earliest Graybullian Eocene to Lostcabinian, with about 930 feet belonging to the Gray Bull equivalent. This was reported by McGrew and Roehler in 1960. A similar sequence of faunules, represented mostly by small isolated teeth, has been found by Roehler on the southeast flank as well, also demonstrating earliest Wasatchian to Lost Cabin time. The lowest faunules here are in beds that strike to the southwest from the Bitter Creek locality. I am particularly indebted to Mr. Roehler for allowing me to study and report on these collections. I look forward to seeing publication of his stratigraphic studies.

SYSTEMATIC DESCRIPTION OF THE MAMMALIA  
MARSUPIALIA

## DIDELPHIDAE

**PERATHERIUM EDWARDI** Gazin

No additional material belonging to the larger and more certainly didelphid of the two species in the La Barge fauna referred to *Peratherium* has been encountered in the Knight. The maxilla and jaw representing this species were both found at the Muddy Creek locality about 12 miles north of Big Piney.

**PERATHERIUM CHESTERI** Gazin

The type lower jaw of this very small species, together with the material of the foregoing form, was discovered at the Muddy Creek locality north of Big Piney. There is, however, a minute jaw in the Princeton University collections (No. 16116) from the Cathedral Bluffs member of the Wasatch to the north of Flat Top Mountain in the Washakie Basin that may be marsupial and possibly represents this species. Morris (1954), in his study of the Cathedral Bluffs fauna, has listed it as *Nyctitherium*, sp. The preserved tooth, as in the La Barge jaw, is the penultimate molar. It is a little smaller and relatively shorter than in the type of *P. chesteri*, but exhibits a similar posterointernally directed hypoconulid, much more lingual in position than in materials that have been referred to *Nyctitherium*, rather more as in marsupials. Confusion as to the identity of the form represented may lie in the appearance of the entoconid, which seems very small and close to the hypoconulid, suggestive in this way of the South American monodelphids although the paraconid and anteroexternal cingulum are not so importantly extended. Examination under  $\times 48$  magnification, however, reveals an irregularly pitted area forward from the hypoconulid, indicating that the greater part of the entoconid may be missing through damage, possibly modified by wear. A better forward development of the entoconid strengthens the suggestion of didelphid affinity. The lower jaw is a little less robust and of slightly less depth than in the type of *P. chesteri*. Neither are sufficiently preserved posteriorward to show the nature of the angle.

**PERATHERIUM MORRISI**, new species

(Plate 1, figure 1)

*Type*.—Right ramus of mandible with two molars, P.U. No. 16115.

*Horizon and locality*.—Cathedral Bluffs member, north of Flat Top Mountain, sec. 4, T. 115 N., R. 93 W., Washakie Basin, Wyoming.

*Description*.—Intermediate in size between *Peratherium chesteri* and *Peratherium edwardi*, but closer to the latter. Talonid basin of lower molars relatively a little shorter and entoconid less developed than in *P. edwardi*.

*Discussion*.—The specimen designated as the type of *P. morrisi* was listed by Morris as *Peratherium*, cf. *P. marsupium*. The teeth are decidedly smaller than in any of the Bridger *P. marsupium* material in the National Museum collections and, as in comparison with *P. edwardi*, the talonid appears relatively shorter. The possibility of the Cathedral Bluffs specimen representing the Bridger species *P. marsupium* seems very questionable.

## INSECTIVORA

### LEPTICTIDAE

#### DIACODON, cf. ALTICUSPIS Cope

The Princeton specimen of *Diacodon*, No. 16171, was cited (1952) as coming from about 100 feet below the Green River beds in the vicinity of Fossil Butte in the Fossil Basin. While the Knight here is regarded as Lysite in age, there remains a possibility that the lowest of these, as west of Elk Mountain, may be Gray Bull in age. There is, however, no faunal evidence to show this. No additional material that may be referred to *Diacodon*, cf. *alticuspis*, has been encountered.

#### PALAEICTOPS, cf. TAURI-CINEREI (Jepsen)

(Plate 1, figure 5)

A portion of a right maxilla with the three molars, U.S.N.M. No. 22122, from the lower Wasatchian horizon at Bitter Creek may well belong to the Gray Bull species *Palaeictops tauri-cinerei* of the Bighorn Basin. The teeth correspond closely in size to those of Jepsen's species, and their structure seems almost identical to that in the type specimen, rather less like *Palaeictops bicuspis* (Cope). In the absence of known upper teeth of *Palaeictops pineyensis*, no comparison with the later Lostcabinian form is feasible, other than to note that the teeth are a little smaller than would be appropriate for good occlusion.

#### PALAEICTOPS PINEYENSIS (Gazin)

(Plate 1, figure 4)

A small jaw fragment with only  $P_3$  preserved, U.S.N.M. No. 22123, and a maxilla with  $M_2$ , U.S.N.M. No. 22444, were collected



since 1952 from the same locality, 12 miles north of Big Piney, as the type of *Palaeictops pineyensis*.  $P_3$  is much longer and exhibits a small anterior, conical cuspule, rather better defined than in *P. tauri-cinerei*, but not as highly placed on the primary cusp as in *Lost Cabin Parictops multicuspis*. The cuspule on the posterior slope of the primary cusp is also conical and well defined, possibly better developed than the posterior or talonid cusp which has been nearly obliterated by wear.

#### LEPTICTID?, genus and species undetermined

An isolated lower molar from low in the Knight to the east of Steamboat Mountain might be  $M_1$  of a leptictid. It is a slender tooth with an elongated trigonid portion, but rather unlike *Diacodon* or *Palaeictops*.

A small jaw in the University of California collection from the Dad locality, No. 43759, exhibits the greater portion of the last two molars. It is much smaller than the foregoing and may be leptictid or possibly nyctitheriid, although resemblance to Bridger forms of the latter seems remote. Damage to critical portions of the teeth leaves much to be desired in attempting a detailed study.

#### ERINACEIDAE?

##### Cf. ENTOMOLESTES, sp.

Isolated teeth that compare very closely with some illustrated by McKenna (1960, figs. 25c, 26) were found by Henry Roehler at various levels in the Knight sequence around the Rock Springs uplift. One upper molar is from west of Rock Springs at a level about 1,195 feet below the Tipton tongue. Roehler considers this to be about Graybullian in age. Another upper tooth found to the southwest of Rock Springs at about 751 feet below this tongue of Green River may be Lysitean although there seems to be no certain evidence of this. A lower jaw fragment with  $M_3$ , which he found above the base of the Tipton tongue on Table Rock to the East of the Rock Springs uplift, is surely Lostcabinian in age.

McKenna (1960, p. 58) has included *Entomolestes* in the family Amphilemuridae, which he regards as insectivore. While this arrangement may be entirely correct, I understand that these and related forms are currently under study by Robinson and by McKenna, so that, until these studies are completed, I have tentatively used the classification employed by Simpson (1945, p. 49). Attention should perhaps be called here to an oversight in Simpson's

citation, in which it is indicated that *Entomolestes* is only lower Eocene in age. This should have included middle Eocene as well, which is the age of the type species.

## PANTOLESTIDAE

### AMARAMNIS,<sup>2a</sup> new genus

*Type*.—*Amaramnis gregoryi*, new species.

*Generic characters*.—Resembling *Palaeosinopa* but lower molars much more slender, and anteroposteriorly elongate trigonids of  $M_2$  and  $M_3$  exhibit more acute anteroexternal angle between paraconid and anterior crest from protoconid. Paraconid more closely joined to metaconid. Talonid basin shallower, cusps less elevated and anterior crest from hypoconid less oblique.

### AMARAMNIS GREGORYI,<sup>3</sup> new species

(Plate 1, figure 2)

*Type*.—Left ramus of mandible with  $M_2$ - $M_3$ , Y.P.M. No. 14702.

*Horizon and locality*.—Lowest beds of Knight member, Gray Bull (Sand Coulee) equivalent,  $1\frac{1}{4}$  miles south of Bitter Creek Station, Sweetwater County, Wyo.

*Specific characters*.—Size near Gray Bull *Palaeosinopa lutreola* Matthew. Specific characters not otherwise distinguished from those cited for the genus.

*Description*.—*Amaramnis gregoryi* is represented only by the type lower jaw, but the peculiarities of the two preserved lower molars readily distinguish it. Although the molars are about the length of those in the type (A.M. No. 15100) of *Palaeosinopa lutreola*, their width is very much less. Perhaps the most noticeable feature of the teeth is the decidedly pentacodontine character of the trigonid portion. The anteroposteriorly elongate trigonid shows a very sharp flexure of the paraconid from the anterior crest of the protoconid, much as in *Pentacodon* and *Coriphagus*, more acute than in *Palaeosinopa*. The cusp arrangement of the talonid, however, more closely resembles that of *Palaeosinopa* and *Pantolestes* with the prominently developed hypoconulid. The basin of the talonid is relatively shallower than in the forms examined, and the crista obliqua is directed more forward, somewhat as in *Pantolestes*, quite unlike *Pentacodon* and *Coriphagus*.  $M_3$  is not reduced as in *Pentacodon* and *Coriphagus*.

<sup>2a</sup> From Latin, *amarus*, *a*, bitter, and *amnis*, small river or stream; with reference to Bitter Creek.

<sup>3</sup> Named for Dr. Joseph T. Gregory who graciously permitted me to study the Marsh Bitter Creek collection.

and the talonid portion is much more elongate as in *Palaeosinopa* and *Pantolestes*.

MEASUREMENTS IN MILLIMETERS OF POSTERIOR LOWER MOLARS  
IN SPECIES OF *Palaeosinopa* AND *Amaramnis*

	<i>P. lutreola</i>	<i>A. gregoryi</i>
	A.M.	Y.P.M.
	No. 15100	No. 14702
	Type	Type
M <sub>2</sub> , anteroposterior diameter: transverse diameter....	3.4:2.8	3.4:2.3
M <sub>3</sub> , anteroposterior diameter: transverse diameter....	4.0:2.8 <sup>a</sup>	3.6:2.2

<sup>a</sup> Approximate.

PALAEOSINOPA, cf. DIDELPHOIDES (Cope)

The lower cheek teeth of the right side, including P<sub>2</sub>-M<sub>3</sub> (U.S.N.M. No. 22453), associated with fragments of the jaw, undoubtedly of *Palaeosinopa*, were found in the New Fork tongue. The lower molars, the first two of which are badly worn so that their length may be slightly less than normal, measure 15 mm. This is very near the measurement of 15.5 mm. given by Matthew (1918) for a specimen of *Palaeosinopa didelphoides*.

Comparison of the New Fork specimen with Bridger *Pantolestes longicaudus* shows the two to be rather close. The premolars are a little longer and more slender, and on M<sub>3</sub>, which is the least worn molar, the paraconid is higher and more lingual in position than in the Bridger specimens observed.

A single lower molar (U.S.N.M. No. 22251), possibly M<sub>2</sub>, from the Cathedral Bluffs tongue on the east side of the Washakie Basin is referred tentatively to Cope's Lost Cabin species. It is about the size of M<sub>2</sub> in the New Fork specimen and has the dimensions given by Matthew (1918, table, p. 590) for this tooth in *P. didelphoides*. It resembles in detail M<sub>2</sub> in the specimen that he figured (1918, fig. 16). Nevertheless, it should be noted that with this very limited material there is little that can be observed to distinguish the Cathedral Bluffs form from Bridger *Pantolestes longicaudus*.

MEASUREMENTS IN MILLIMETERS OF TEETH IN LOST CABIN  
AND NEW FORK SPECIMENS OF *Palaeosinopa*

	<i>P. didel-</i> <i>phoides</i>	<i>P., cf. didel-</i> <i>phoides</i>
	A.M.	U.S.N.M.
	No.	No.
	4804	22453
	Type	
P <sub>3</sub> , anteroposterior diameter: transverse diameter....		5.0:2.1
P <sub>4</sub> , anteroposterior diameter: transverse diameter....		5.4:2.5
M <sub>1</sub> , anteroposterior diameter: transverse diameter....	5.2:3.4	5.0:3.5
M <sub>2</sub> , anteroposterior diameter: transverse diameter....	5.5:3.9	5.1:4.0
M <sub>3</sub> , anteroposterior diameter: transverse diameter....	6.3:3.6	5.5:3.2



**PALAEOSINOPA, sp.**

Several isolated teeth of *Palaeosinopa* from the Bitter Creek locality in both the National Museum and Marsh collection indicate a species decidedly smaller than Gray Bull *P. veterrima*. They are only a little smaller than in *P. didelphoides*, but the type of Cope's species is from the Lost Cabin beds, so that there may be some doubt as to its presence in the lowest horizon of the Knight. The isolated upper molars from Bitter Creek are relatively much narrower than in *P. veterrima* and show much less development of the cingulum. Two lower premolars, Y.P.M. No. 14700, are a little shorter than in *P. veterrima* and much more slender. Matthew cites narrower lower molars for *P. didelphoides* but the dimensions he gives for  $M_2$  (1918, p. 590) would indicate that this tooth is relatively wider than in *P. veterrima*. The Bitter Creek teeth may well represent a distinct species but the materials known are clearly inadequate for diagnosis under the circumstances.

**APATEMYIDAE****APATEMYS HÜRZELERI,<sup>4</sup> new species**

(Plate 2, figure 7)

*Type*.—Right ramus of mandible with I,  $M_2$ , and the talonid portion of  $M_1$ , U.S.N.M. No. 22386.

*Horizon and locality*.—La Barge faunal horizon (Lost Cabin equivalent), 12 miles north of Big Piney, Sublette County, Wyo.

*Specific characters*.—Size appreciably larger than Gray Bull *Teilhardella chardini* Jepsen, close to Bridger *Apatemys bellulus* Marsh, but molars distinctly narrower.

*Description*.—Only the type lower jaw of *Apatemys hürzeleri* is known. Much of the bone is missing but the incisor is complete. Also the second molar and the posterior portion of the first are preserved. I am in agreement with McKenna that this form should be referred to *Apatemys* rather than *Teilhardella*.

The large lower incisor is decidedly procumbent. Its crown portion shows enamel on the outer surface and on the lower or anterior part of the medial side. Along the outer margin of the concave upper surface of the tooth crown the upper margin of the outer enamel shows slight or subdued serration. The dorsoventral and transverse diameters of this tooth just posterior to the crown, about where the tooth would emerge from the alveolus, are 2.5 and 1.4 mm. respec-

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<sup>4</sup> Named for Dr. Johannes Hürzeler in recognition of his work on apatemyids.

tively. In the type of Gray Bull *Teilhardella chardini* these measurements, near the same position, are about 2.05 and 1.15 mm.

The bone of the jaw is broken away anterior to the forward root of  $M_1$ , so that there is no information concerning the roots of  $P_4$ .  $M_2$  is characterized by a comparatively high crest formed by the protoconid and metaconid, but the anterior crest of the trigonid is very subdued and the paraconid is decidedly weaker than evident in later apatemyids. The talonid basin, moreover, is rather shallow.  $M_2$  is much larger than would have been included in the type of *T. chardini* (P.U. No. 13236). Its anteroposterior and transverse measurements are 2.0 and 1.3 mm. respectively. No direct comparison with this earlier apatemyid is feasible as only  $P_4$  and  $M_3$  are preserved in the Princeton specimen. Nevertheless, the combined length of  $M_1$  and  $M_2$  as measured at the alveoli can be compared, and in *T. chardini* this is 2.7 mm. whereas in *A. hürzeleri* it is 3.4 mm.

*A. hürzeleri* is rather close in size to Bridger *Apatemys bellulus*. The incisor has about the same dimensions at the alveolus as in A.M. No. 12048 and  $M_2$  is about the same length as in A.M. No. 12048 or as in Marsh's type, Y.P.M. No. 13513. Its width, however, is very much less. Also in *A. hürzeleri* the paraconid of  $M_2$  is distinctly lower and weaker, the crest of the talonid in both  $M_1$  and  $M_2$  is lower and the outer walls of the teeth do not bulge outward at the cingulum so markedly as in the type of *A. bellulus*.

The La Barge form is only a little larger than the earlier and geographically more remote *Teilhardella whitakeri*. The dimensions of  $M_2$  given by Simpson (1954, p. 4) are 1.7 and 1.2 mm. for the anteroposterior and transverse diameters respectively. Moreover, the depth of jaw below  $M_2$  on the lingual side is given as 3.6 mm. This depth in the La Barge specimen is 4.8 mm.

## PRIMATES

### NOTHARCTIDAE

#### PELYCODUS, cf. TRIGONODUS Matthew

Three lower jaw portions and a third upper molar from the Bitter Creek locality seem close to the species *Pelycodus trigonodus* that Matthew described from the Gray Bull horizon in the Bighorn Basin. The lower molars are indistinguishable from those in Gray Bull lower jaws in the National Museum collection referred to this species.  $P_4$  in U.S.N.M. No. 22256, however, seems relatively a little larger than noted in the Gray Bull specimens; nevertheless, in Y.P.M. No. 14075 the correspondence in the size of this tooth is very close.

Fragments of a pair of lower jaws (U.S.N.M. No. 22258) with  $M_2$  and  $M_3$  from the lower part or Gray Bull horizon of the Knight escarpment to the southwest of Elk Mountain in the Fossil Basin correspond closely to the above Bitter Creek material and are also tentatively referred to *P. trigonodus*. Possibly isolated teeth from the Red Desert locality east of Steamboat Mountain represent the same species. Their size is in accordance.

#### PELYCODUS, near *P. JARROVII* (Cope)

Four jaws and a maxilla from the slopes of Fossil Butte in the Fossil Basin nearly all exhibit distinctly larger teeth than in the Bitter Creek specimens. These may also represent *Pelycodus trigonodus* but would appear to represent at least a more advanced mutant. The larger of these can be closely matched in proportions of teeth in Gray Bull materials tentatively identified as *Pelycodus jarrovi*. There may be some doubt, however, as to whether *P. jarrovi*, originally based on New Mexican material, should be recognized in Wyoming, but if it is, earlier *P. trigonodus* may be distinguished from it on scarcely more than an arbitrary size range, or, as in the case of Bridger *Notharctus tenebrosus* and *Notharctus robustior*, by an arbitrary stratigraphic limit. It may be further noted that the species of *Pelycodus* represented in the exposures around Fossil Butte exceeds in size *Notharctus limosus* of the La Barge fauna, but not *N. venticolus*.

The maxilla (U.S.N.M. No. 22259) from the saddle to the north of Fossil Butte is rather close in size to the type of *P. trigonodus*, but shows better evidence for a hypocone on the molars. In the latter respect it can be closely matched in somewhat larger Bighorn Basin specimens referred to *P. jarrovi*. It is particularly close in both size and development of a hypocone crest to A.M. No. 4174 labeled "small form of *Pelycodus jarrovi*" from an undetermined level in the Bighorn Basin.

#### PELYCODUS? PRAETUTUS,<sup>5</sup> new species

(Plate 4, figures 2-4)

*Type*.—Right ramus of mandible with  $P_3$  (incomplete)- $M_2$ , U.S.N.M. No. 22262.

*Horizon and locality*.—Gray Bull (Sand Coulee) equivalent of Knight,  $1\frac{1}{4}$  miles south of Bitter Creek Station, Sweetwater County, Wyo.

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<sup>5</sup> From Latin, *prae*, before, and Cope's species *P. tutus*.



*Specific characters.*—Much smaller than *Pelycodus? tutus* Cope, but resembles it in most of the following: Lower molars elongated. Trigonid decidedly narrow with paraconid well separated from metaconid in both  $M_1$  and  $M_2$ . Talonid basin broad, deep, and comparatively smooth. Posterior crest from hypoconid swings down to cingulum posterointernally and is separated from the entoconid by a deep notch. Entoconid high, relatively conical and forward in position. It joins the metaconid by a high, laterally flexed crest.

*Material.*—In addition to the type (pl. 4, fig. 4) there is a portion of the left ramus of a mandible with  $P_2$ - $P_4$  (Y.P.M. No. 14697; pl. 4, fig. 2) and a jaw fragment with  $M_3$  (Y.P.M. No. 14698; pl. 4, fig. 3), probably not of the same individual, in Marsh's collection from the Bitter Creek locality. An isolated lower molar, evidently  $M_2$ , from the Red Desert locality east of Steamboat Mountain, also belongs to this form.

*Discussion.*—The characters of the lower molars, first noted by Cope (1877, p. 141) and later by Matthew (1915c, p. 441) for *Pelycodus tutus*, and here observed in *P.? praetutus*, are so very distinctive in comparison with Gray Bull, Lysite, and other San Jose and lower Knight material that there might seem justification in recognizing a distinct genus, were it not for the striking variability of these features in later *Notharctus*. While the paraconid seems progressively lowered or reduced in much of the material of *Notharctus*, the talonid largely retains the form seen in *Pelycodus trigonodus* but with the greater isolation of the entoconid from the posterior crest, particularly in  $M_2$ , approaching, although not quite reaching, the condition seen in *P.? tutus* and *P.? praetutus* as an extreme. Nevertheless, typical *Pelycodus* apparently exhibits greater stability in these features and the *P.? praetutus*-*P.? tutus* line seems rather distinctive in comparison with contemporaries.

#### NOTHARCTUS LIMOSUS Gazin

(Plate 4, figure 5)

Several additional jaws, maxillae, and isolated teeth belonging to *Notharctus limosus* have been obtained from Knight exposures beneath the Fontenelle tongue in the vicinity of Big Piney and La Barge. These do not, however, yield any new information beyond that covered in the earlier report.

A maxilla (P.U. No. 16123) with  $M^1$ - $M^3$ , collected by Morris from Knight beds beneath the Tipton tongue near Dad, Wyo., resembles *N. limosus* in general form and in the relative width (trans-

versely) of the upper molars but is appreciably smaller, being more nearly comparable in size to *Pelycodus ralstoni*. The length of the upper molar series in this specimen is 10.8 mm., whereas in *N. limosus*, U.S.N.M. No. 19293, the comparable measurement is 12.8 mm. Moreover, both the hypocone and mesostyle in the Princeton specimen may be just a little less developed. The precise horizon for this specimen is not known; possibly it came from low in the section.

A maxilla and jaw fragment found by Henry W. Roehler about 416 feet below the Tipton tongue on the southeast flank of the Rock Springs uplift may well represent *N. limosus*. While  $P^4$  in the maxilla is a little larger than this tooth in the figured specimen (1952, pl. 1, fig. 6) of *N. limosus*, the molars correspond rather closely. Moreover,  $M_2$  in the jaw fragment has a length comparable to that in specimens of *N. limosus*, which is less than in *N. nunienus*, but its relative width seems unusual for either form.

#### NOTHARCTUS, cf. NUNIENUS (Cope)

Various lower jaws and isolated teeth of *Notharctus* found in the New Fork beds are consistently larger than any of the specimens representing *Notharctus limosus* in the La Barge fauna. These may well represent the Lost Cabin species *N. nunienus*. The size of the teeth compares very favorably with Cope's species.

#### NOTHARCTUS, cf. VENTICOLUS Osborn

The material representing the larger species of *Notharctus*, *N.*, cf. *venticolus*, in the La Barge fauna has been increased by about six lower jaw portions and two maxillae. Only one or possibly two jaw fragments with single teeth appears to be of the same species in the New Fork fauna. However, a lower jaw (U.S.N.M. No. 22254) with  $M_1$  and  $M_2$  and two isolated molars from the Cathedral Bluffs tongue near Flat Top Mountain on the east side of the Washakie Basin seem almost identical to certain of the La Barge specimens of this form. No. 22254 is only slightly larger than the type of *N. venticolus*. The specimen (P.U. No. 16109) cited by Morris (1954, p. 197) as *Notharctus*, sp., from the Cathedral Bluffs, was cataloged in the Princeton collections as *Notharctus venticolus*. It exhibits an  $M_2$  that can also be closely matched in the La Barge material of *Notharctus*, cf. *venticolus*, although it is a little smaller than in No. 22254 from these beds.

#### NOTHARCTUS, sp.

A lower jaw (U.S.N.M. No. 22255) with  $P_3$ - $M_2$  from beds believed to be a part of the Cathedral Bluffs tongue, on the northwest



side of Oregon Buttes, is only a little larger than the New Fork material referred to *N. nunienus*, but seems too small for *N. venticolus*. The teeth can be matched for size in Bridger material of *Notharctus tenebrosus*, and nearly matched in general form of the molars, but the identity is rather uncertain and such an assignment would be unwarranted.

## OMOMYIDAE

### OMOMYS SHEAI,<sup>6</sup> new species

(Plate 2, figures 3 and 4)

*Type*.—Right ramus of mandible with  $M_2$ - $M_3$ , U.S.N.M. No. 22384.

*Horizon and locality*.—La Barge local fauna, Lost Cabin equivalent, 12 miles north of Big Piney, Sublette County, Wyo.

*Specific characters*.—Size of lower molars between Gray Bull *Omomys vespertinus* Matthew and Lysite *Omomys minutus* Loomis. Trigonid of lower molars a little less elevated and a little better basined than in *O. vespertinus*. Talonid basin relatively narrower.

*Description*.—Although intermediate in size between *Omomys vespertinus* and *Omomys minutus*, *Omomys sheai* is close to *O. vespertinus* and might well fall within the size range of the latter, recalling the variation in this respect of Bridger *Omomys carteri*. The crowns of the teeth, however, seem to be a little more advanced in the direction of *Omomys carteri* in that the trigonids of the lower molars do not appear to be as elevated on the outer sides and their apices show a tendency toward distinct basining seen in Bridger material.

A second jaw portion (U.S.N.M. No. 19197; pl. 2, fig. 3) with only  $M_3$ , was questionably referred to *Absarokius* in 1952 (p. 24). The tooth is nearly identical in size to this molar in the type of *O. sheai* and may well represent this species. It differs only in that the trigonid is slightly shorter, anteroposteriorly, and the paraconid is somewhat weaker and a little more medial in position.

Loomis's *Omomys minutus* (pl. 2, fig. 5) would seem correctly allocated to *Omomys* although nothing is known of the premolars of this decidedly small species. The molars exhibit high and delicate-appearing cusps and the trigonid is rather elevated in comparison with the better-known middle Eocene material. Although it has a stratigraphic position intermediate between the type of *O. vespertinus*

<sup>6</sup> Named for George Shea of Billings, Mont., who graciously aided in the field in 1949.

*tinus* and Knight *O. sheai*, it does not form an intermediate stage between them. It is of further interest to note that the talonid basins in the lower molars of all the Wasatchian *Omomy*s materials are somewhat elongated, but rather less so than in Bridgerian materials. They do not appear, however, to be relatively so short as in upper Wasatchian *Loveina* (pl. 2, fig. 1). The trigonid pattern clearly separates *O. minutus* from *Anemorhysis*.

#### OMOMYS, cf. VESPERTINUS Matthew

(Plate 5, figure 2)

A lower jaw fragment with  $M_1$  and  $M_2$  in the University of Wyoming collection (No. 1647) from the Red Desert locality east of Steamboat Mountain is a little larger than *Omomy*s *sheai*.  $M_2$  is very much like that in *O. sheai*, but its length is nearly the same as that in Graybullian *Omomy*s *vespertinus*, which is more nearly equivalent in age. The width of the talonid portion of the tooth, however, is a little less than in *O. vespertinus*, and relatively a little narrower than in *O. sheai*, although the difference here is less evident. Suggestive of *O. vespertinus* is the somewhat higher outer wall of the lower molars than in *O. sheai*.

#### MEASUREMENTS IN MILLIMETERS OF LOWER MOLARS IN WASATCHIAN SPECIES OF *Omomy*s

	<i>O. vespertinus</i> A.M.N.H. No. 16835 Type	<i>O. minutus</i> A.C.M. No. 3365 Type	<i>O. sheai</i> U.S.N.M. No. 22384 Type
$M_1$ - $M_3$ length .....	7.8	5.8	
$M_1$ , anteroposterior diameter:			
transverse diameter .....	2.6:2.0	2.0:1.6 <sup>a</sup>	
$M_2$ , anteroposterior diameter:			
transverse diameter .....	2.4:2.0	1.9:1.6	2.2:1.8
$M_3$ , anteroposterior diameter:			
transverse diameter .....	2.7:1.7	2.2:1.3	2.6:1.5

<sup>a</sup> Approximate.

#### CHLORORHYSIS KNIGHTENSIS Gazin

(Plate 2, figure 2; plate 12, figure 10)

This interesting omomyid in the La Barge fauna was described in 1958 from the anterior portion of a lower jaw exhibiting C- $P_4$ , but the molars were not then known. It was considered close to *Loveina* but differences in  $P_3$  and  $P_4$ , particularly in the absence of a postero-internal crest extending from the primary cusp of  $P_3$ , and in the

weaker posterointernal crest and weaker and much lower position of the metaconid of  $P_4$ , as discussed in 1958 (p. 27), seemed to warrant separate recognition.

A lower jaw (U. of C. No. 46705) from the Dad locality, recently sent to me by McKenna, surely represents this species. It was found about 6.9 miles north of Baggs in a yellow weathering claystone approximately 100 feet below the Tipton tongue.  $P_4$  in this specimen is so completely like that in the type of *Chlororhysis knightensis* that I have no hesitancy in referring it to this form. It seems, moreover, to demonstrate the characters of the lower molars not previously known.

$M_1$  in the Dad specimen (pl. 12, fig. 10) is a little smaller than in *Loveina zephyri* and the posterior wall of the trigonid where it is joined by the crista obliqua is simpler and more nearly flat. In *Loveina* the posterior wall of the trigonid is offset and the crista obliqua joins it in the deepest part of the indentation. Also, the posterior wall lingual to the crista obliqua is more rugose or plicate. The talonid basin of  $M_1$  in *Chlororhysis* is shallower and the surrounding crest is smoother with less emphasis on the separate cusps. In *Loveina* the hypoconulid of  $M_1$  is separated from the nearby hypoconid by a notch which is essentially missing in *Chlororhysis*. Moreover, the pair of crests from both the protoconid and hypoconid in *Loveina* seem to form a sharper V. In *Chlororhysis* these form a more blunt angle or a better U shape.

The trigonid is damaged in  $M_2$  of the Dad specimen but the talonid exhibits essentially the same broad but shallow basin and comparatively even surrounding crest as in  $M_1$ .  $M_3$  is about the length of  $M_2$  but noticeably narrower with a rapidly tapering talonid. The trigonid portion of  $M_3$  is relatively short anteroposteriorly but exhibits a small paraconid in a nearly lingual position.

A second specimen from La Barge, a jaw fragment with only  $M_1$  (U.S.N.M. No. 22385), had been cataloged as *Loveina zephyri* but it shows a much closer correspondence to the  $M_1$  in the Dad specimen of *Chlororhysis knightensis*. It seems advisable at this point, in view of the rarity of *Loveina zephyri* specimens, to note that the Lost Cabin lower jaw, U.S.N.M. No. 18439, described by White (1952, p. 193) as belonging to *L. zephyri*, is undoubtedly of *Absarokius noctivagus*, so that the information there furnished regarding posterior molars does not apply to Simpson's species.

It is of further interest to note that although *Chlororhysis* is near *Loveina*, which seems rather typically omomyid, the differences

from it, though not great, are rather generally toward the anaphomorphids, somewhat suggestive of *Absarokius* in the character of  $P_4$  although this tooth is not nearly so enlarged. This would seem to add another instance to the maze of developmental trends that tend to complicate taxonomy, emphasizing its arbitrary nature, particularly noticeable in the Primate order.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN  
*Chlororhysis knightensis*

	U.S.N.M. No. 22385	U.S.N.M. No. 21901 Type	U. of C. No. 46705
C, anteroposterior diameter at cingulum .....		1.1	
$P_2$ , anteroposterior diameter: transverse diameter .....		1.3:1.0	
$P_3$ , anteroposterior diameter: transverse diameter .....		1.8:1.4	
$P_4$ , anteroposterior diameter: transverse diameter .....		2.0:1.7	2.0:1.8
$M_1$ , anteroposterior diameter: transverse diameter .....	2.1:1.7		2.2:1.7
$M_2$ , anteroposterior diameter: transverse diameter .....			2.3 <sup>a</sup> :1.7
$M_3$ , anteroposterior diameter: transverse diameter .....			2.4:1.5

<sup>a</sup> Approximate.

## ANAPTOMORPHIDAE

### ANEMORHYSIS SUBLETTENSIS (Gazin)

(Plate 3, figure 1)

Following description of *Anemorhysis sublettensis* (1952, p. 24) as a possible form of *Paratetonius*, it was realized that the type of *Paratetonius*, *P. steini*, was not distinct from *Tetonius homunculus*. As a consequence the name *Anemorhysis* was proposed (1958, p. 25) for the La Barge form and to this genus was allocated the Lysite species "*Tetonius*" *musculus* Matthew (pl. 3, fig. 2). No new material of *A. sublettensis* has come to light but specimens representing a form that may be closely related were found in the lowermost beds of the Knight near Bitter Creek. These are described below.

### TETONOIDES,<sup>7</sup> new genus

*Type*.—*Tetonoides pearcei*, new species.

*Generic characters*.—Resembling *Tetonius* but  $P_4$  relatively much

<sup>7</sup> From its resemblance to *Tetonius*.



smaller and lower crowned, with much better-developed paraconid and metaconid, better-defined talonid and well-defined external cingulum. Lower molars *Tetonius*-like but labial wall with a relatively much shorter slope and a well-developed cingulum. Apex of trigonid in lower molars transversely narrower and less compressed antero-posteriorly than in *Anemorhysis*.

**TETONOIDES PEARCEI,<sup>8</sup> new species**

(Plate 3, figures 3-5; plate 5, figure 1)

*Type*.—Right ramus of mandible with  $P_3$ - $M_2$ , U.S.N.M. No. 22426.

*Horizon and locality*.—Lowest beds of Knight member, Gray Bull (Sand Coulee) equivalent,  $1\frac{1}{4}$  miles south of Bitter Creek Station, Sweetwater County, Wyo.

*Specific characters*.—Size of teeth very close to those of "*Tetonius*" *tenuiculus* Jepsen, but paraconid and metaconid of  $M_2$  and  $M_3$  distinctly closer together, and anterior crest from protoconid on these teeth with greater anteroexternal deflection.

*Material*.—In addition to the type (pl. 5, fig. 1), which includes the posterior premolars as well as the anterior molars, there are two jaws that exhibit all three molars (U.S.N.M. No. 22382, see pl. 3, fig. 4; and U.S.N.M. No. 22799), a jaw with only  $M_2$  but exhibiting the anterior alveoli (U.S.N.M. No. 22383, see pl. 3, fig. 3), and a jaw portion with  $P_3$  and  $P_4$  (Y.P.M. No. 14084, see pl. 3, fig. 5) and the more forward alveoli. All of these except for No. 22799 were found at the Bitter Creek locality. No. 22799 was collected by Henry W. Roehler from a level 1,126 feet below the Tipton tongue on the west side of the Rock Springs uplift, in association with *Haplomylus*.

Among the Gray Bull materials with which comparisons were made are three lower jaws that beyond doubt represent Jepsen's "*Tetonius*" *tenuiculus* which I am here referring to *Tetonoides*. One of these, A.M. No. 15066 with  $P_4$ - $M_2$  (pl. 3, fig. 6), questionably referred by Matthew to "*Tetonius*" *musculus*, is, as Jepsen's type, from low in the Gray Bull. A specimen in the National Museum, U.S.N.M. No. 19154 (pl. 3, fig. 7), with  $M_2$  and  $M_3$  from Elk Creek, also may well be from low in the Gray Bull but this is uncertain. A third lower jaw was recently observed in the collections at Princeton University. The molars in these jaws bear a strong resemblance to those in *Tetonius homunculus*, but with the differences noted above, and are of a size to occlude well with the type upper teeth of *Tetonoides tenuiculus*. Additional correspondence with the type of *T. tenuiculus*

<sup>8</sup> Named for Franklin L. Pearce who aided me on so many field expeditions.



is seen in the relatively smaller fourth premolar than in *Tetonius homunculus*.

*Description*.—The formula for the lower dentition of *Tetonoides pearcei* is  $\bar{2}, \bar{1}, \bar{3}, \bar{3}$ . The anterior incisor is enlarged but moderately erect, as in *T. homunculus*, and the second of the two incisors is small with its elongate root posterolateral to the other. The canine alveolus is of moderate size with a more nearly circular outline than the others. An alveolus for a  $P_2$  is only a little smaller than that of the canine in the type and in Y.P.M. No. 14084, but anteroposteriorly more flattened in U.S.N.M. No. 22383. The presence of  $P_2$  in *T. pearcei* is a rather primitive feature in comparison with *Tetonius homunculus*, as it is for anaptomorphids in general, and may well be suspected for *T. tenuiculus* also, although none of the known lower jaws of the latter is sufficiently complete to determine this feature. Larger *T. homunculus* with its relatively larger  $P_4$  shows no evidence of a  $P_2$ .  $P_3$  in *T. pearcei* is two-rooted and only a little smaller than  $P_4$ . It lacks the metaconid seen on  $P_4$ , and the small paraconid is not deflected inward as in  $P_4$ .  $P_4$  has the relatively very small size characterizing *T. tenuiculus*, but the outer wall at the cingulum is a little longer anteroposteriorly. The paraconid appears a little higher on  $P_4$  and the metaconid lower and perhaps less developed than in *T. tenuiculus*, as represented by A.M. No. 15066. The talonid of  $P_4$  is much alike in the two species. It is of further interest to note that the external cingulum of  $P_4$ , and of the lower molars as well, is better developed in both *T. pearcei* and *T. tenuiculus* than in *T. homunculus*. Usually  $P_4$  and  $M_1$  in *T. homunculus*, with their vertically more elongate outer wall, show little or no evidence of the external shelflike cingulum conspicuous in the smaller form.

Although the lower jaws of *Tetonoides pearcei* and *T. tenuiculus* are alike in certain details, including size, in which they differ from *T. homunculus*, the molar trigonids ( $M_2$  and  $M_3$ ) appear to be significantly different between the two smaller species. While the inner and outer walls of the crowns converge upward, almost as noticeably as in *T. homunculus*, so that the apex of the trigonid is relatively narrow—in comparison, for example, with *Anemorhysis sublettensis*—the paraconid in *T. pearcei* is rather closer to the metaconid than it is in *T. tenuiculus*. In this respect the crown resembles *Anemorhysis*. Also it was noted that the crest from the protoconid in the posterior lower molars makes a more pronounced anteroexternal deflection as it extends from the protoconid to the anterior margin of the paraconid. This condition, together with the shorter distance between the apices

of the paraconid and metaconid, gives the trigonid a somewhat less triangular appearance than in *T. tenuiculus*.

Were it not for the more noticeable upward convergence of the inner and outer walls of the lower molars, *T. pearcei* might well have been referred to *Anemorhysis*. *A. sublettensis*, a slightly smaller form, otherwise shows a shorter and broader trigonid and a relatively longer talonid. Anteroposterior development of the talonid also characterizes  $P_4$  in *A. sublettensis*.  $M_3$  in *Anemorhysis muscula* is very close in size to this tooth in *T. pearcei* (U.S.N.M. Nos. 22382 and 22799), and although  $M_3$  is not known in *A. sublettensis*, the anteroposteriorly shorter trigonid and slightly more erect outer wall of the protoconid strongly suggest that *A. muscula* is more properly referred to *Anemorhysis* than to *Tetonoides*. I strongly suspect that *Tetonoides* is close to the line of development for *Anemorhysis*.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH OF  
*Tetonoides pearcei* AND *Tetonoides tenuiculus*

	<i>T. pearcei</i>			<i>T. tenuiculus</i>	
	Y.P.M. No.	U.S.N.M. No.	U.S.N.M. No.	A.M. No.	U.S.N.M. No.
	14084	22382	22383	15066	19154
$P_2$ - $P_4$ (at alveoli).....	2.8		2.7		
$M_1$ - $M_3$ , inclusive .....		5.4			
$P_3$ , anteroposterior diameter:					
transverse diameter .....	1.3:1.0				
$P_4$ , anteroposterior diameter:					
transverse diameter .....	1.5:1.3			1.5:1.4	
$M_1$ , anteroposterior diameter:					
transverse diameter .....		1.8:1.5		1.8:1.6	
$M_2$ , anteroposterior diameter:					
transverse diameter .....		1.7:1.6	1.8:1.6	1.8:1.7	1.7:1.6
$M_3$ , anteroposterior diameter:					
transverse diameter .....		2.2:1.4			2.1:1.3

**ABSAROKIUS, near A. ABBOTTI (Loomis)**

(Plate 5, figure 3)

A lower jaw from the Red Desert area, that McGrew assures me is from the Gray Bull level, is found to represent *Absarokius* rather than *Tetonius*. The specimen (U. of Wyo. No. 1644, see pl. 5, fig. 3), collected by Henry W. Roehler in SW $\frac{1}{4}$ NE $\frac{1}{4}$  sec. 10, T. 24 N., R. 100 W., includes  $P_3$ - $M_3$  and exhibits all the alveoli anterior to  $P_3$ . The molar teeth are relatively small but can be matched in a particularly small specimen of *A. abbotti* (A.M. No. 14672) from the Lysite, but  $P_4$  in the Red Desert specimen is a little larger. The relatively

larger size of  $P_4$  is rather suggestive of Lost Cabin *Absarokius noctivagus*. This combination of characters indicates, if the horizon is correctly recorded, that the development of  $P_4$  may be rather variable and not so orderly with respect to horizons of Wasatchian time.

The University of Wyoming specimen has two incisor alveoli, the first of which may be a trifle larger and more nearly circular in outline than the second. The canine alveolus is distinctly larger than that for the second incisor but evidently no greater in size than that for the anterior root of  $P_3$ . None of these are comparable to that for the enlarged anterior tooth in *Tetonius*. Between the canine alveolus and the anterior root of  $P_3$  there may possibly be an extremely flattened alveolus for a  $P_2$ , only slightly narrower transversely than that for the canine.  $P_3$  would appear from outside the jaw to have two well-defined roots.

MEASUREMENTS IN MILLIMETERS OF TEETH IN LOWER JAW OF  
*Absarokius*, near *A. abbotti*, U. OF WYO. NO. 1644

$M_1$ - $M_3$ , length of lower molars.....	6.1
$P_3$ , anteroposterior diameter: transverse diameter at cingulum.....	1.5:1.8
$P_4$ , anteroposterior diameter: transverse diameter at cingulum.....	2.4:2.5
$M_1$ , anteroposterior diameter: transverse diameter at cingulum.....	2.3:1.8
$M_2$ , anteroposterior diameter: transverse diameter at cingulum.....	2.0:1.7
$M_3$ , anteroposterior diameter: transverse diameter at cingulum.....	2.1:1.4

**ABSAROKIUS NOCTIVAGUS** Matthew

(Plate 4, figure 1)

Among the more recently acquired materials representing *Absarokius noctivagus* is a maxilla (U.S.N.M. No. 22264) with  $P^3$ - $M^3$  from the locality 12 miles north of Big Piney.  $P^2$ , a very small, peglike tooth, was present in maxilla when found, but unfortunately it has since been lost.  $P^3$ , much smaller than  $P^4$ , is seen to be three-rooted with a prominent deuterococone and the talon is somewhat expanded posteriorly, almost as in  $P^4$ . This specimen, as well as the immature lower jaw previously described (1952, p. 24), was discussed in 1958 (pp. 73-74) in connection with the possible dental formula characterizing anaptomorphids. The lower jaw was illustrated in 1958 (pl. 14, fig. 8), whereas a drawing of the upper dentition is included here (pl. 4, fig. 1).

**ABSAROKIUS WITTERI** Morris

The Cathedral Bluffs species described by Morris is clearly larger and with a more inflated-appearing  $P_4$  than in *Absarokius noctivagus*.



Also, as Morris has pointed out, the molar talonid basins are more strongly crenulated. Only the type specimen, a lower jaw (P.U. No. 14972), has been discovered. The three species *A. abbotti*, *A. noctivagus*, and *A. witteri* would seem to present a gradational sequence characterized principally by the development of  $P_4$ , except for the rather unusual specimen from the early Wasatchian of the Red Desert.

**UINTASOREX, cf. PARVULUS Matthew**

(Plate 5, figure 4)

A minute jaw fragment with  $M_2$  and  $M_3$  (U. of Wyo. No. 1646), lent to me by Paul McGrew, is described as coming from a locality of Lost Cabin age in the Red Desert region. The specimen corresponds well in size with the type of *Uintasorex parvulus* (A.M. No. 12052) although the same teeth are not included. It is about intermediate in size of the posterior molars between the Yale specimen (No. 13519) and jaw portions from the "Upper Fossiliferous Horizon" of the Green River at the Powder Springs locality in the Uinta Basin. Correspondence to *Uintasorex* is seen in the anteroposteriorly abbreviated trigonid, the large *Omomys*-like talonid and the distinctive *Cynodontomys*-like notch between the entoconid and closely adjacent hypoconulid of  $M_2$ . It resembles the Green River material somewhat more than the Yale Bridger specimen in the less constricted and less projecting hypoconulid of  $M_3$ , but perhaps differs from both in less evidence of an external cingulum on the two molars.

This form is clearly related to, but much smaller than, McKenna's (1960) *Niptomomys doreenae* from the Four Mile fauna, although the latter has relatively wider talonid basins. A somewhat closer correspondence is seen to the specimen described as Cf. *Niptomomys doreenae* in the less widely expanded talonid basins and in the appearance of the cingulum, but differs from it in that Cf. *Niptomomys doreenae*, though smaller than the Four Mile type, is somewhat larger than the Red Desert specimen and shows a more discernable, lingually placed paraconid on both of the molars, which, incidentally, look very much alike.

**PHENACOLEMURIDAE**

**PHENACOLEMUR, cf. PRAECOX Matthew**

(Plate 2, figure 6)

*Phenacolemur* is so far represented in the Knight only in the Bitter Creek fauna. A single specimen (Y.P.M. No. 14062), a lower jaw portion with  $M_2$  and the posterior crest of the talonid of  $M_1$ , is pre-

served. Some of the bone is missing along the lower part of the jaw, exposing the root portion of the enlarged incisor. The jaw is rather close in size to contemporary material of *Phenacolemur praecox* from the Bighorn Basin and may be tentatively referred to this species. It does, however, show differences worthy of comment. The trigonid of  $M_2$  seems a little narrower and the protoconid and metaconid are more conical and less developed as a transverse crest. Also, the talonid basin is slightly longer and shallower, and there is less of a notch anterior to the entoconid. Although these and certain other related features seem rather important, there would appear from Simpson's discussion (1955) to be considerable variation in Gray Bull materials included in *P. praecox*. Should it be demonstrated, however, that the distinctive features of the Bitter Creek specimen were persistent in a larger sample, their significance might be on a generic level.

## MIXODECTIDAE

### CYNODONTOMYS ANGUSTIDENS Matthew

(Plate 1, figure 6)

*Cynodontomys* material from the lower part of the Knight member near Bitter Creek Station includes a maxilla with  $M^1$  and  $M^2$  (U.S.N.M. No. 22121) and a lower jaw with  $M_1$  and  $M_2$  (U.S.N.M. No. 22446) collected by Smithsonian Institution parties and, in addition to a couple of isolated teeth, a lower jaw with  $P_3$ - $M_3$  (Y.P.M. No. 14696) collected by Marsh's party. These specimens seem almost certainly to be of *Cynodontomys angustidens* described by Matthew on Gray Bull Material.

The upper molars in U.S.N.M. No. 22121 (pl. 1, fig. 6) lack the mesostyle seen in later species, although the external cingulum rises slightly at about this position.  $M^1$  is very much like that in the specimen of *C. angustidens* figured by Matthew (1915c, p. 477, fig. 48) but is somewhat smaller and exhibits a slightly weaker hypocone.

The fourth premolar of the lower series in the Yale specimen is a little broader than in the type of *C. angustidens* and shows a moderately well-developed metaconid that is rather close to the protoconid and not as high. It is, however, a little higher and more widely separated from the protoconid than in the type. The talonid of  $P_4$  has a decidedly narrow basin but exhibits a distinct hypoconid and entoconid. There appears, however, to be no evidence for a hypoconulid. The lower teeth in Y.P.M. No. 14696 are distinctly smaller than in the type of *Cynodontomys latidens* and the metaconid of  $P_4$  is not as large and upstanding.



An isolated  $M_3$  from north of Tipton Butte corresponds closely in size to the above material and suggests that the beds in that area may be relatively low in the Knight.

#### CYNODONTOMYS KNIGHTENSIS Gazin

(Plate 1, figure 7)

In addition to 11 lower jaws, 4 maxillae have been added to the collection representing *Cynodontomys knightensis* in the La Barge fauna. These were obtained in 1953, 1954, and 1959, all from the Muddy Creek locality 12 miles north of Big Piney, Wyo. Two of the maxillae, U.S.N.M. Nos. 22106 (pl. 1, fig. 7) and 22107, include  $P^4$ - $M^3$  complete.  $P^4$ , though smaller than in *C. scottianus*, exhibits a slightly more constricted lingual portion than shown in the specimen figured by Matthew (1915c, p. 472, fig. 42). This tooth, however, shows much less disparity in size and possibly a better separation of the primary cusp and tritocone (paracone and metacone) than in *C. latidens*. The molars, moreover, exhibit a conspicuous mesostyle and the hypocone on  $M^1$  and particularly  $M^2$  is well developed.

#### CYNODONTOMYS SCOTTIANUS (Cope)

(Plate 1, figure 8)

Five lower jaws, together with portions of both maxillae of a sixth individual, have been found in the New Fork beds to the east of Big Piney, Wyo. The teeth in all these are fully as large as in typical *Cynodontomys scottianus* of the Lost Cabin beds, distinctly larger than in *Cynodontomys knightensis*, which occurs beneath the Green River tongue separating the two horizons in this area.

The maxillae above referred to (U.S.N.M. No. 22117; pl. 1, fig. 8) include  $P^1$ - $P^4$  on one side, as well as  $M^2$ , and  $P^4$ - $M^3$  on the other.  $P^1$  and  $P^2$  are simple, nearly equal teeth with partially divided roots.  $P^3$  is a triangular, three-rooted tooth with a very small deuterocone and no tritocone. The latter may not be significant however, because, although Matthew (1915c, p. 474, fig. 44) shows the tritocone on  $P^3$  of a specimen of *Cynodontomys latidens*, it is not invariably present in Bridger *Microsyops*.  $P^4$  is comparable in size with  $M^1$  but shows a noticeably longer labial portion and a relatively narrower lingual portion than illustrated by Matthew (1915c, p. 472, fig. 42). This tooth is much like that in earlier *C. knightensis* but with a relatively more robust primary cusp. The upper molars in U.S.N.M. No. 22117 are a little larger than in observed Lost Cabin material of *C. scottianus*, except for a specimen in the American Museum col-

lections (A.M. No. 2969) labeled "*C. scottianus* but a little larger," and the hypocone is noticeably weaker. The hypocone, particularly that of  $M_2$ , is much weaker than in *Cynodontomys knightensis*.

The New Fork jaw material referred to *Cynodontomys scottianus* is comparatively robust and  $P_4$  relatively large, particularly in the breadth of this tooth in two individuals. In comparison with *Cynodontomys knightensis*,  $P_3$  is large but with an actually smaller talonid. The trigonid portion of  $P_4$  appears more robust and with relatively greater anteroposterior development than in the earlier species. The metaconid is more posterior relative to the protoconid than is usual in *C. knightensis*; moreover, the talonid of this tooth is highly variable and shows a cusp arrangement that does not so nearly conform to that of the molars. The New Fork species is evidently much smaller than *Cynodontomys lundeliusi* White.

#### CYNODONTOMYS, sp.

The lower jaw from Knight Station (A.M. No. 12836), which Granger considered as suggesting Lysite, has been labeled *Cynodontomys latidens*?. As indicated in 1952, the absence of premolars leaves some doubt as to the specific reference. Its size, however, is about right for that species.

### TILLODONTIA

#### ESTHONYCHIDAE

##### ESTHONYX, cf. BISULCATUS Cope

Isolated upper teeth of *Esthonyx*, which may be referred to *E. bisulcatus*, were found by George Pipiringos at a locality just to the north of Tipton Butte and much farther north at a lower level in the Knight east of Steamboat Mountain. A lower molar, collected by our 1954 expedition from the lowest beds of the Knight exposed to the west of Elk Mountain in the Fossil Basin, may also be of this species.

##### ESTHONYX, cf. ACUTIDENS Cope

(Plate 1, figure 3)

Two more isolated teeth from localities to the south of Big Piney have been added to the materials representing the larger species of *Esthonyx* in the La Barge fauna.

Additional esthonychid materials from the New Fork member, including a lower jaw (U.S.N.M. No. 22124; pl. 1, fig. 3) with  $Dp_1$  and the first two molars, shows that a somewhat larger variant of *Esthonyx acutidens* than that in the La Barge fauna is represented in the New Fork fauna. The lower molars are noticeably high crowned and the talonid portions are large, as characteristic of the Lost Cabin species. The teeth in No. 22124 are of a size that permits good occlusion with upper teeth in the rostral portion of a skull from the Lost Cabin figured in 1953 (Gazin, p. 26, fig. 8).

**ESTHONYX, sp.**

An upper fourth premolar in the Princeton collection, No. 16129, is reported to be from the "Hiawatha" member exposed north of Baggs, Wyo., on the east side of the Washakie Basin. It is comparatively small for *Esthonyx acutidens*, smaller than would be expected in the Dad local faunule, and the tritocone is rather weakly defined for either *E. acutidens* or *E. bisulcatus*. The horizon in the "Hiawatha" member is not given. Possibly the specimen came from beds as low as those worked by McKenna to the south of Baggs.

No further material of *Esthonyx* than that mentioned in 1952 was found in the type section for the Knight near Knight station.

**TROGOSUS?, cf. LATIDENS (Marsh)**

The last upper molar of the large tillodont *Trogosus* was recorded by Morris (1954, pl. 21, fig. 1) as coming from the Cathedral Bluffs member of the Wasatch on the east side of the Washakie Basin, sec. 4, T. 15 N., R. 93 W. The tooth was originally identified by me and thought to be strong evidence of a Bridgerian age for the Cathedral Bluffs beds. An earlier record in which a similar isolated tooth of an advanced tillodont, possibly of the same form, collected by Nace (1939) in beds regarded as Cathedral Bluffs in the Red Desert region to the north, was identified by Simpson as "*Tillotherium*" and likewise believed to be Bridgerian. I am now convinced, from the evidence presented by the associated fauna, that the Cathedral Bluffs beds are of Lostcabinian or late Wasatchian age and that *Trogosus* was not restricted to Bridgerian time but evidently appeared earlier, although there is no evidence to show that it was actually associated in the same horizon with *Esthonyx*. There would seem to be, however, too much difference between these forms in the Cathedral Bluffs to postulate evolution in situ.

## TAENIODONTA

### STYLINODONTIDAE

#### ECTOGANUS, sp.

(Plate 12, figure 7)

Three lower teeth, including  $Dp_4$  and portions of two molars, seem almost certainly to represent *Ectoganus*. They were found on an exposure of Knight in the Fossil Basin, immediately to the west of the saddle which separates Fossil Butte from the Green River capped table to the north. The  $Dp_4$  corresponds very closely to this tooth in the type of *E. gliriformis*, as well as to a  $Dp_4$ , showing only slightly greater wear, in the jaw belonging to the Gray Bull skull (U.S.N.M. No. 12714) that I described in 1936. The two molar teeth are incomplete but show no wear, so that I suspect they may be  $M_2$  and  $M_3$  rather than  $M_1$  and  $M_2$  as here illustrated (pl. 12, fig. 7). There is some suggestion in the height of cusps, distribution of enamel, and separation of roots that the teeth may be very slightly higher crowned,  $Dp_4$  as well as the molars, than in the type or in the Gray Bull specimen. It is of further interest to note that the tooth thought to be  $M_3$  shows a slight paraconid and a hypoconulid somewhat as in the teeth figured by Wortman (1897, fig. 24) as "*Calamodon simplex*." None of the comparatively unworn molars in U.S.N.M. No. 12714 shows evidence of a hypoconulid. This is evidently a variable feature.

#### Undetermined STYLINODONT

No further information is forthcoming as to the generic identity of the stylinodont skeleton from the locality in the La Barge horizon north of Big Piney, described in 1952. It may well be *Stylinodon*, as this genus has been recorded in Lost Cabin beds of the Wind River Basin, as well as in the Bridger formation. There is no certainty, however, that earlier *Ectoganus* did not persist as such into later Wasatchian time.

## EDENTATA

### EPOICOTHERIIDAE?

#### PENTAPASSALUS PEARCEI Gazin

There has been no additional material discovered of this small armadillo-like edentate in the La Barge fauna, although a metacarpal of a somewhat longer-toed form in the Bitter Creek fauna is discussed below.



**Undetermined palæanodont edentate**

Dr. Peter Robinson has recently brought to my attention an edentate toe bone that he encountered during his curatorial work on the Eocene collections at Yale Peabody Museum. It has Marsh's field No. 888 and was collected by J. Heisey in 1876 at Bitter Creek. The specimen is a third metacarpal from the left foot. The proximal extremity very closely resembles that in McIII of *Pentapassalus pearcei* and has about the same diameter. It is, however, about 25 percent longer, the shaft appears a little more slender, and the tubercle for the pars brevis of the extensor muscle is not nearly so robust. In comparison with the forefoot of much larger *Metacheiromys dasypus* figured by Simpson (1931) the dorsal margin of the proximal articular facet does not appear to be deflected so far distally on the shaft, and the lateral portion of the proximal extremity shows very little surface for articulation with the unciform.

**RODENTIA****PARAMYIDAE**

Most of the paramyid material from the various localities and horizons in the Wasatch has been examined by Dr. A. E. Wood, as a part of his study of this rodent family, and recognition of the following genera and species result from identifications he has furnished me of the better materials.

**PARAMYS EXCAVATUS Loomis**

(Plate 4, figure 8)

This comparatively small species of *Paramys* would appear to be represented only in the La Barge and lower levels of the Knight. Two lower jaws were obtained from the exposures low on the escarpment to the west and southwest of Elk Mountain in the Fossil Basin and one jaw (see pl. 4, fig. 8) came from the Bitter Creek locality. A lower jaw in the collection of Miller and Granger shows this species is represented in the horizon at Knight Station. Five lower jaw portions and a maxilla have been added to the La Barge collection, so that the species is now represented by 10 specimens in the later fauna.

**PARAMYS COPEI Loomis**

*Paramys copei* is rather well represented in the La Barge fauna and two additional jaws and a maxilla have been added to the collection since 1952.

Specimens from the Washakie Basin that I have tentatively referred to this species include a left mandibular ramus with  $M_1$ - $M_3$ , U.S.N.M. No. 22419, and an isolated lower molar in the University of California collection from the Knight escarpment beneath the Tipton tongue between Dad and Baggs, Wyo. There is, moreover, a specimen, U.S.N.M. No. 22420, that includes a jaw portion and three associated lower teeth from the Cathedral Bluffs on the west side of the basin, that may be this species.

#### PARAMYS MAJOR Loomis

A maxilla with  $P^4$  and  $M^1$  (U.S.N.M. No. 22414) collected at the Muddy Creek locality north of Big Piney in 1954, has teeth of a size that indicate that a third specimen now represents large *Paramys major* in the La Barge fauna. Two lower jaws in the Princeton collection (Nos. 16106 and 16127), from beneath the Tipton tongue south of Dad, are also surely of this species.

I have not found this species in Knight beds older than Lost Cabin, but the New Fork beds above the Fontenelle tongue have produced at least five specimens that would appear to be referable to it. From the Cathedral Bluffs of the Washakie Basin a single isolated upper tooth in the Princeton collection corresponds well in size.

#### REITHROPARAMYS, sp.

A single lower jaw with only  $M_2$  preserved, U.S.N.M. No. 22380, from the saddle north of Fossil Butte in the Fossil Basin, is regarded by Wood as representing a species of *Reithroparamys*, near a form that he is describing as new in his forthcoming study of the family.

#### MICROPARAMYS, sp.

A lower jaw in the Princeton collection from the Cathedral Bluffs beds, U.P. No. 16112, is recognized by Wood as representing this genus. Description of the species represented is to appear in his report.

### SCIURAVIDAE

#### KNIGHTOMYS SENIOR (Gazin)

(Plate 5, figures 5 and 6)

The genus *Knightomys* was proposed (Gazin, 1961) for the La Barge species that had originally been described as *Tillomys senior* in 1952. The generic characters may again be summarized as follows: Lower cheek teeth anteroposteriorly short, broad across talonid and

very low crowned. Cusps low and conical. Talonid basin large but very shallow and trigonid basin scarcely discernable. Except for posterolophid, the transverse lophs are comparatively weak and ill defined. The mesoconid is clearly defined and there is a distinct hypoconulid.

New material of *Knightomys senior* includes a pair of lower jaws (U.S.N.M. No. 22415) with  $P_4$ - $M_2$  on right and  $M_2$ - $M_3$  and a part of  $M_1$  on the left ramus. The upper teeth are not known.  $P_4$  is narrow across the trigonid but was evidently bicuspid. The talonid of this tooth has a shallow basin and the entoconid is simple and conical. A slight ectolophid and better-defined posterolophid join the hypoconid of  $P_4$  in the type, U.S.N.M. No. 19308, but these are scarcely evident in No. 22415. There is no mesoconid on  $P_4$ . The molar trigonids are low and anteroposteriorly short with only the slightest evidence of an anterolophid or even a cingulum, and this only on  $M_1$ . Although the teeth in neither of the two preserved specimens are unworn, the saddle between the protoconid and metaconid, except for a slight depression in  $M_1$ , shows no evidence of a trigonid basin. The ectolophid is very weak but the conical mesoconid is distinct. This cusp does not have a crest extending lingually. The entoconid is nearly conical but does have a weak crest extending a short distance into the basin toward the hypoconid, but falls far short of reaching this cusp. The hypoconid sends a more distinctive posterolophid postero-internally, clearly separated from the entoconid and its weak spur. The posterolophid is moderately worn on the specimens at hand but there is clear evidence of a distinct hypoconulid.

Material of *Knightomys senior* seems without doubt to be closer to *Tillomys? parvidens* than to any other sciuravid. However, comparison with  $M_2$  in U.S.N.M. No. 17701 of *T.? senex* from the lower Bridger and with the figure of the type of *T.? parvidens*, Y.P.M. No. 13350, given by R. W. Wilson (1938, fig. 12), reveals that *K. senior* has lower-cusped teeth with less development of transverse lophids.  $M_2$  is only slightly smaller than in the Bridger material at hand, but the trigonid appears less elevated and shorter anteroposteriorly. Also, the mesoconid is more nearly conical and the posterolophid does not project so far lingually. The teeth of *Tillomys senex*, figured by Wilson (1938, fig. 10), seem more remote, as the weak spur from the entoconid in *K. senior* does not reach the hypoconid or the posterolophid as in the American Museum specimen. It should be noted, however, that this *T. senex* specimen shows more advanced wear. As observed by Wilson, *Tillomys? parvidens*, and I



might add *Knightomys senior*, shows a development between paramyids and typical sciuravids. The resemblances would seem to be toward, for example, the Cathedral Bluffs *Microparamys* and decidedly away from such forms as *Mysops*.

#### DAWSONOMYS WOODI Gazin

(Plate 5, figure 7)

*Dawsonomys woodi* was proposed (Gazin, 1961) as a new genus and species for the La Barge form represented by the lower jaw (U.S.N.M. No. 19309) that was cited in 1952 as "*Sciuravus*, possibly *S. depressus* Loomis." The generic characters may again be summarized as follows: Cusps of teeth low, but with metaconid of  $P_4$  high and well forward. Trigonid of  $M_1$  broad and anteroposteriorly compressed, but with small, distinct trigonid basin. Talonid basin large and comparatively shallow. Ectolophid low with distinct mesoconid. Entoconid low and lophid from entoconid low but well defined and joins hypoconid. Posterolophid extends nearly to lingual margin and close to but sharply separated from the crest extending buccally from the entoconid.

The species was observed to be appreciably smaller than *Sciuravus nitidus* but diagnostic characters at this level were not otherwise distinguished from those cited as characterizing the genus.

Direct comparison of the type of *Dawsonomys woodi* with the lower jaw that Loomis cited as a cotype of "*Sciuravus*" *depressus* has indicated that they do not represent the same species and clearly not the same genus.  $M_1$  in the Lysite jaw (A.C.M. No. 458, see pl. 5, fig. 9) has a much narrower trigonid, a larger talonid basin, and the mesoconid is more marginal in position. The most noticeable difference, however, is in the lophid from the entoconid which is weaker, much closer to the posterolophid, and appears scarcely more than a slight bifurcation of the posterolophid at the hypoconulid. In the latter respect the Lysite jaw rather resembles  $M_1$  in the Cathedral Bluffs *Microparamys* jaw (P.U. No. 16112).

Loomis's type of "*Sciuravus*" *depressus* is a skull (A.C.M. No. 432) portion with three molars preserved (see pl. 5, fig. 8) and while no direct comparison between *D. woodi* and the upper teeth of "*S.*" *depressus* can be made, the pattern of the latter seems surely sciuravid rather than paramyid. The crests of the upper teeth are subdued, but I note that the metaconulid joins the metaconid, possibly somewhat more as in *Taxymys* than as in *Sciuravus*. Kelley and Wood (1954) have noted that Loomis's species does not belong to *Sciuravus*.



*Dawsonomys woodi* is a much larger form than *Knightomys senior* and is distinctly more *Sciuravus*-like, but like *K. senior* its teeth have lower cusps and relatively larger talonid basins than *Sciuravus nitidus*.  $P_4$  in *D. woodi* has a well-developed protoconid and metaconid, rather widely separated and decidedly oblique in arrangement. The talonid has a large but shallower basin than in *S. nitidus*. There does not appear to be a mesoconid on this tooth, but the crest extending buccally from the entoconid is somewhat more molarlike than noted in the Bridger species.

Measurements of teeth of *Dawsonomys woodi* have been included with those of *Sciuravus wilsoni*.

### SCIURAVUS WILSONI Gazin

(Plate 4, figures 6 and 7)

The type specimen of *Sciuravus wilsoni* is the right ramus of a mandible with  $P_4-M_2$  (U.S.N.M. No. 22425), found in the New Fork horizon on the west side of Alkali Creek, near the center of T. 29 N., R. 110 W., in Sublette County, Wyo. The species, described as new in 1961, was characterized as being intermediate in size between *Sciuravus nitidus* and *Sciuravus bridgeri*, close in this respect to *Dawsonomys woodi* of the La Barge fauna. Talonid basins of the lower molars are smoother and less complicated than in the Bridger forms. No trace of a mesolophid or a crest from the mesoconid was noted, and there is little or no evidence of a metastylid. Teeth were cited as being in general less progressive in appearance than in *S. nitidus*.

The size of the teeth in the type of *Sciuravus wilsoni* is much less than in the bulk of the Bridger material referred to *Sciuravus nitidus* but only slightly less than in specimens of the least size included in that species. The teeth are, however, significantly larger than in the type of *Sciuravus bridgeri*. In details of the tooth crowns *S. wilsoni* makes a much closer approach to *Sciuravus nitidus* than does earlier *Dawsonomys woodi*. The higher cusps and deeper folding of basins and valleys closely resembles that in *S. nitidus*. The talonid basins, however, are uncomplicated, as the mesolophid is lacking, and in the type there is no metastylid, features that may be developed to varying degrees in the Bridger material.

In addition to the type lower jaw there is a right maxilla, U.S.N.M. No. 22424, with  $M^1-M^3$  somewhat worn, from the same locality. It corresponds closely in size for proper occlusion with teeth in the type of *S. wilsoni*. Although wear has reduced the principal lingual cusps to confluent or nearly confluent enamel lakes, the buccal wall and cusps are essentially like those in *S. nitidus*.

Several isolated sciuravid teeth from the Cathedral Bluffs (in a vial accompanying a *Notharctus* jaw, P.U. No. 16109) are tentatively referred to *S. wilsoni*. These are a part of the evidence cited by Morris (1954, p. 199) as indicative of a Bridgerian age. Some of the lower teeth are a little larger than in the New Fork jaw, and in certain of them there is noted a little better evidence for a metastylid. Nevertheless, they resemble those in *S. wilsoni* in having a somewhat less progressive appearance than in *S. nitidus*. An upper molar in this assortment of teeth from the Cathedral Bluffs is about the size of those in the New Fork maxilla but is much less worn, and it is observed that the metaloph is not so deflected anteriorly, resulting in a relatively smaller basin between the metaloph and posterior cingulum than in *S. nitidus*. There is, of course, no certainty that the teeth are all of the same sciuravid.

MEASUREMENTS IN MILLIMETERS OF UPPER AND LOWER TEETH IN  
WASATCHIAN SCIURAVIDS \*

	" <i>Sciuravus</i> " <i>depressus</i>	<i>Sciuravus</i> <i>wilsoni</i>
	A.C.M. No. 432 Type	U.S.N.M. No. 22424
Length, M <sup>3</sup> -M <sup>2</sup> , inclusive.....	5.4	5.5
M <sup>1</sup> , anteroposterior diameter: transverse diameter ...	1.7: 1.8	1.7: 2.0
M <sup>2</sup> , anteroposterior diameter: transverse diameter...	1.7: 1.8	1.8: 2.1
M <sup>3</sup> , anteroposterior diameter: transverse diameter...	1.9: 1.7	2.0: 2.0
	" <i>Sciuravus</i> " <i>depressus</i>	<i>Dawsonomys</i> <i>woodi</i>
	A.C.M. No. 458 "Cotype"	U.S.N.M. No. 19309 Type
		<i>Sciuravus</i> <i>wilsoni</i>
		U.S.N.M. No. 22425 Type
Length, P <sub>4</sub> -M <sub>2</sub> , inclusive.....		5.7
P <sub>4</sub> , anteroposterior diameter:		
transverse diameter .....	1.9: 1.5	1.9: 1.6
M <sub>1</sub> , anteroposterior diameter:		
transverse diameter .....	1.9: 1.7	2.0: 1.8
M <sub>2</sub> , anteroposterior diameter:		
transverse diameter .....		2.1: 1.9

\* Measurements of the type of *Knightomys senior* were given in 1952 (p. 49).

## CARNIVORA

### ARCTOCYONIDAE

#### THRYPTACODON, near T. ANTIQUUS Matthew

No additional material of *Thryptacodon*, beyond that from the La Barge horizon described in 1952, has been encountered in any of the Knight horizons.

## MESONYCHIDAE

## HAPALODECTES COMPRESSUS Matthew

(Plate 8, figure 6)

Portions of both rami of a mandible of the rare mesonychid *Hapalodectes compressus* were found in the New Fork beds on Alkali Creek (Sublette County). The teeth of this specimen, U.S.N.M. No. 22447, are somewhat damaged but a sufficient portion of each remains to demonstrate their exceedingly slender character. Comparison with the type of *H. compressus* (A.M. No. 12781) from the Lysite shows that the New Fork specimen is comparable in length of teeth and in the depth and slenderness of the jaw, and would not be confused with heavier-jawed *Hapalodectes leptognathus*. The teeth, if anything, are more slender than in the *H. compressus* type, or even than in the Lost Cabin jaw (A.M. No. 14748) that Matthew noted as having more slender teeth and a shallower jaw than the type.

## PACHYAENA OSSIFRAGA Cope

A number of broken pieces of skull and associated jaw and tooth portions (U.S.N.M. No. 22449) from the Bitter Creek locality are referred to Cope's New Mexican species *Pachyaena ossifraga*. Among these is the greater part of an upper molar, lacking only the deuterocone, that corresponds remarkably well in size and various other details with Cope's type (U.S.N.M. No. 1096), presumably an M<sup>1</sup>.

## PACHYAENA GRACILIS Matthew

About 15 associated teeth (U.S.N.M. No. 22448) of *Pachyaena* were found in the Gray Bull equivalent of the Knight near the base of the escarpment west of Elk Mountain in the Fossil Basin. These compare very closely in size with various teeth in the type of *Pachyaena gracilis* (A.M. No. 15728) from the Gray Bull beds in the Bighorn Basin. Their size, nevertheless, is but little less than in the *P. ossifraga* material. An upper molar, possibly M<sup>1</sup>, in addition to smaller size, shows somewhat less development of the metacone than in the type of *P. ossifraga*.

An incomplete lower cheek tooth from low on the slope of Fossil Butte may also represent *P. gracilis*. It is, however, rather small and somewhat suggestive of earlier *Dissacus*.

## PACHYAENA?, sp.

No additional material believed to represent *Pachyaena*, other than the two specimens reported in 1952, has been found in the New Fork

beds. Matthew (1915b, pp. 87-88) did not encounter this genus in beds later than Gray Bull, although Loomis reported it from later beds in the Bighorn Basin. The two lower teeth from the New Fork horizon were thought to be of a size appropriate for *P. gracilis*. They could, nevertheless, be referred with equal conviction to *P. ossifraga*.

## OXYAENIDAE

### OXYAENA, sp.

Further material of *Oxyaena* in the collections from the La Barge horizon includes a  $P_4$  and the anterior part of  $M_2$  associated (U.S.N.M. No. 22450). The premolar is as long as in *Oxyaena forcipata* but both teeth are a little more slender. They are also slightly more rugose than in the type material. Comparison with *Oxyaena pardalis* is difficult, inasmuch as the critical talonid portion of the molar is not preserved; but size would appear to exclude this Lost Cabin species, as well as *Patriofelis* (*Protopsalis*) *tigrinus*, from consideration.

The earlier (1952) described specimen of *Oxyaena*, a first lower molar in the Princeton collection (No. 16176) from near La Barge, was regarded as more nearly comparable in size to *Oxyaena lupina*. There is no certainty, of course, that the two La Barge specimens represent the same species. So far as the other horizons are concerned, only an isolated lower premolar from the Bitter Creek locality and another from the Dad locality are believed to be *Oxyaena*. The Bitter Creek tooth corresponds very closely in size and other details to  $P_3$  in the type of *Oxyaena lupina*. In the absence of other evidence, however, recognition of *Oxyaena lupina* in the Bitter Creek fauna would not be warranted. The Dad tooth may be  $P_2$  and corresponds well, except for a little greater width, with this tooth in *Oxyaena forcipata*, the possibility, however, of its representing *Patriofelis* should not be overlooked.

### AMBLOCTONUS, cf. MAJOR Denison

To the National Museum materials representing *Ambloctonus* there have been added an  $M_1$ , with the top of the trigonid missing, and an incomplete premolar from the La Barge horizon in the Big Piney area. These may well belong to the same species as that represented by the Princeton jaw (P.U. No. 14720) described in 1952. A lower premolar, probably  $P_2$  in the Princeton collection from the Dad locality (P.U. No. 16125) seems also to represent Denison's (1938) Lost Cabin species *Ambloctonus major*.



## LIMNOCYONIDAE

## PROLIMNOCYON ELISABETHAE Gazin

(Plate 6, figure 6)

New material of *Prolimnocyon elisabethae* includes a right maxilla (U.S.N.M. No. 22454) with  $P^4$  and  $M^4$  from the Muddy Creek locality 12 miles north of Big Piney, in the La Barge horizon. The teeth are almost identical to those in U.S.N.M. No. 19348 figured in 1952 so that no new information is added. Moreover, Kelley and Wood (1954) have referred to this small though advanced species a right maxilla with  $P^4$ - $M^3$  from the Lysite horizon in the Wind River Basin.

No dimensions for the teeth of *P. elisabethae* were given with the original description. These are included in the table of measurements accompanying the discussion of the following species.

## PROLIMNOCYON, cf. ANTIQUUS Matthew

(Plate 6, figure 5)

A pair of lower jaws, U.S.N.M. No. 22452, much more robust and with larger teeth than *Prolimnocyon elisabethae* were encountered in the New Fork horizon of the Wasatch. Both jaws are preserved from the canine alveolus to about the masseteric fossa. The left ramus included  $P_4$ - $M_2$ , whereas the right ramus has preserved only  $P_2$ ,  $M_2$ , and the heel of  $M_1$ . The length of the tooth row is about the same as in the type of *Prolimnocyon antiquus*, and like this species, as well as *P. elisabethae*, has a single alveolus for the root of  $M_3$ . Unlike *P. elisabethae*, which has a very slender and shallow jaw, the depth of the New Fork jaws is even greater than in *P. antiquus*. They are not comparable in this respect, however, to Gray Bull *Prolimnocyon robustus*. The weakness of the parastylid on  $P_4$  is also more as in Lost Cabin referred material of *P. antiquus* than as in *P. elisabethae*.  $M_1$  is more slender than the tooth accompanying the type of *P. antiquus*. Matthew evidently has this accompanying tooth shown in the position of  $M_1$  in the drawing of *P. antiquus*, but I am convinced that this loose tooth does not represent *Prolimnocyon* but belongs to *Vulpavus*. The talonid portion of  $M_2$  is also a little more slender than in the preserved portion of this tooth in the type of *P. antiquus*.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN  
SPECIMENS OF *Prolimmocyon*

	<i>P. atavus</i>	<i>P. elisabethae</i>	<i>P. antiquus</i>	<i>P. antiquus</i>
	A.M. No. 16816 Type	U.S.N.M. No. 19350 Type	A.M. No. 14768 Type	U.S.N.M. No. 22452
P <sub>1</sub> -M <sub>3</sub> (at alveoli).....		35.0	41.0	40.0
P <sub>1</sub> -P <sub>4</sub> (at alveoli).....		20.6	25.3	25.0
M <sub>1</sub> -M <sub>3</sub> (at alveoli).....	14.0	14.0	15.5	15.0
P <sub>2</sub> , anteroposterior diameter:				
transverse diameter ....		5.0:2.1		4.9:2.1
P <sub>3</sub> , anteroposterior diameter:				
transverse diameter ....		5.4:2.0		
P <sub>4</sub> , anteroposterior diameter:				
transverse diameter ....		5.8:2.6		6.3:2.9
M <sub>1</sub> , anteroposterior diameter:				
transverse diameter ....	6.2:3.4	5.9 <sup>a</sup> :3.0 <sup>a</sup>		6.4:3.5
M <sub>2</sub> , anteroposterior diameter:				
transverse diameter ....	6.4:4.2	6.8:3.5		7.0:4.0
M <sub>3</sub> , anteroposterior diameter:				
transverse diameter ....	2.6:1.7			

<sup>a</sup> Approximate.

## HYAENODONTIDAE

### SINOPE, possibly *S. VIVERRINA* (Cope)

(Plate 6, figure 3)

A pair of lower jaws (U.S.N.M. No. 22456) of a decidedly small species of *Sinopa* was found in the La Barge level of the Knight beds about 12 miles north of Big Piney. Most of the teeth are preserved although some are slightly damaged. Direct comparison with Cope's type of the New Mexican species *Sinopa viverrina* is not feasible because, not only were there no lower teeth included, but the palatal portion, exhibiting the upper dentition figured by Cope (1877, pl. 38, fig. 1), has been missing from the type material (U.S.N.M. No. 1022) for some time. Nevertheless, from the measurements given by both Cope and Matthew for these upper teeth, it seems that the proportions of the lower teeth in the Knight specimen are entirely compatible for proper occlusion.

The lower molars in No. 22456 are characterized by talonids having a very weak, posteriorly placed entoconid and almost no lingual crest or ridge forward from the entoconid position. The talonid basin slopes steeply to the lingual margin of the tooth, reaching a climax in M<sub>3</sub> where the narrow, elongate talonid is essentially without a basin. It may be further noted that the anterior premolars follow the canine

with very short or almost no diastema in comparison with jaws from the same horizon tentatively referred to *Sinopa vulpecula*.

**SINOPA, cf. MULTICUSPIS (Cope)**

(Plate 6, figure 4)

A Bitter Creek lower jaw (U.S.N.M. No. 22459) with  $M_1$  and  $M_2$  preserved is tentatively referred to *Sinopa multicuspis*. The lower teeth in the Bitter Creek jaw occlude very well with the upper molars in the type and are not significantly different in size from teeth in New Mexican specimens referred by Cope to this species. A correspondence was also noted in size of teeth to the type of *Sinopa secundaria*, although the latter has more slender lower jaws. On the other hand, *Sinopa mordax* has deeper jaws and a more reduced  $M_3$  than indicated in the Bitter Creek specimen. Considering the wide range of sizes and characters shown in materials of *Sinopa* and the plethora of species that have been proposed, *S. mordax* may not actually be distinct from *S. multicuspis*. A careful reexamination of all the materials of *Sinopa* is much needed, as the present taxonomic arrangement seems illogical.

To *Sinopa multicuspis* is also tentatively referred a right maxilla, with portions of two molars, U.S.N.M. No. 22460, from high on Fossil Butte and fragments of isolated teeth from this locality and from west of Elk Mountain in the Fossil Basin.

**SINOPA, cf. VULPECULA Matthew**

(Plate 6, figures 1 and 2)

The best of the Knight material (U.S.N.M. No. 19347) compared to Matthew's small Lost Cabin species was described in 1952. A couple of specimens that represent the same species have been added to the La Barge collection but these do not furnish new information.

Two maxillary portions, one of these with  $P^4$  and the other (U.S.N.M. No. 22462) with  $M^2$  and  $M^3$ , from the New Fork tongue are also thought to be of *Sinopa vulpecula*. The teeth are no larger than in *Sinopa multicuspis* but the molar talons seem more robust. In this connection it may be noted that the talonids of the lower molars in the La Barge material compared to *S. vulpecula* also seemed relatively broader than in the various Knight materials that were referred to *S. multicuspis*.

**SINOPA, cf. STRENUA (Cope)**

No additional material of a larger species thought to represent *Sinopa strenua* was encountered in the La Barge-Big Piney area, but

an assortment of associated upper and lower teeth with jaw and other fragments (U.S.N.M. No. 22461) from the earlier or Gray Bull equivalent about 4 miles to the southwest of Elk Mountain in the Fossil Basin may also represent this species. The upper teeth of this specimen are noticeably larger than in either *Sinopa multicuspis* or *S. vulpecula*, whereas the lower teeth compare very favorably with the type of *S. strenua*.

## MIACIDAE

### DIDYMICTIS PROTENUS (Cope)

(Plate 7, figure 3)

Among the materials that might logically be referred to earlier Wasatchian *Didymictis protenus* is a lower jaw portion with  $P_4$  and  $M_1$  (U.S.N.M. No. 22457) from the Bitter Creek locality. The size of  $M_1$  appears to be close to that in Cope's type from New Mexico, as measured at the roots, inasmuch as only the talonid portion of this tooth is preserved in the type (U.S.N.M. No. 1092).  $P_4$ , however, is a little larger. Its principal cusp, moreover, is a little higher. Simpson (1937, p. 14) has noted considerable variation in size of materials in the Gray Bull referred to *D. protenus*.

This species seems also to be represented by tooth fragments from the Gray Bull equivalent of the Knight west of Elk Mountain in Fossil Basin.

A remarkably good skeleton of *Didymictis* (P.U. No. 14917) from about 15 miles north of Baggs, Wyo., is in the Princeton collection. It is from the Knight beds just below the Tipton tongue, but is unusually small for this horizon. Measurements of the teeth are only a trifle larger than in the type of *D. protenus* to which it is very tentatively referred. The possibility of its falling near the lower limit of the range in size for the small mutant of *D. altidens* should be considered. Nevertheless, its size is well below the range noted for the La Barge materials. The specimen is to be described in detail elsewhere.

### DIDYMICTIS ALTIDENS Cope

(Plate 7, figures 1 and 4)

The reasons for referring the La Barge *Didymictis* materials to *D. altidens* were discussed in 1952. The few specimens added to this collection since that time furnish no further information. The sample shows somewhat less variability than the Gray Bull materials,



and in comparison with the type of *D. protenus* the La Barge form exhibits distinctly larger teeth and much deeper jaws.

Among the newer collections from the New Fork tongue there is, in addition to several isolated tooth fragments, a large jaw (U.S.N.M. No. 22458) with damaged teeth associated with some fragments of a skull. These are of a form averaging larger than that represented by the La Barge materials, as might be expected in single species showing progressive increase in size.

As isolated  $M_1$  in the Princeton collection from the Cathedral Bluffs (P.U. No. 16113), here figured (pl. 7, fig. 4) in comparison with La Barge and Bitter Creek specimens, is scarcely larger (only 0.2 mm. longer at the roots) than this tooth in the New Fork jaw. It would appear to be close to typical *D. altidens*.

Some fragments of teeth from the higher slopes of Fossil Butte are of a moderately robust form, tentatively referred to *D. altidens*. This is in keeping with the interpretation proposed by Simpson (1937, p. 15) that Matthew's Lysite subspecies (mutant) should probably be included in *D. altidens*.

#### VIVERRAVUS, cf. ACUTUS Matthew

(Plate 7, figure 9)

A right ramus of the mandible with  $P_4$  and  $M_1$  (U.S.N.M. No. 22465) and a second specimen with only  $P_4$  from the Bitter Creek locality are found to be of a species of *Viverravus* distinct from *V. lutosus* of the later horizons of the Wasatch. The teeth are smaller, particularly the premolars, than in *V. lutosus*, and the talonid basin of the carnassial appears relatively narrower. The two specimens correspond more closely to *Viverravus acutus*, and  $P_4$ , particularly in the second specimen, is very little different in size.  $M_1$  in No. 22465, however, appears somewhat smaller and relatively more slender than this tooth, which is incomplete, in the lower Gray Bull or Sand Coulee type. The teeth in all but one of the other Gray Bull jaws observed are indeed larger than in the type. Nevertheless, the differences are not great and the Bitter Creek materials may be tentatively referred to this species, although they may possibly represent a small mutant.

A lower carnassial in the collections of the University of California (No. 43821) from the Knight about 11 miles north of Baggs, Wyo., and between 100 and 150 feet below the Tipton tongue is surprisingly close to  $M_1$  in the above Bitter Creek jaw. It cannot be referred to *V. lutosus* although the horizon represented seems characterized by that species. It is also tentatively allocated to *V. acutus*.

**VIVERRAVUS LUTOSUS** Gazin

(Plate 7, figures 5 and 7)

Fragments of three jaws and a maxilla, each with a single tooth, have been added to the materials representing *Viverravus lutosus* in the La Barge fauna. The species is now also represented by a lower jaw (U.S.N.M. No. 22464) with  $M_2$  and the talonid portion of  $M_1$  from the New Fork tongue (pl. 7, fig. 7). The preserved part of  $M_1$  agrees very closely with this tooth in the type but  $M_2$  is perhaps a trifle smaller than in certain referred specimens from the Muddy Creek locality north of Big Piney. It is also noted that the Cathedral Bluffs lower jaw (P.U. No. 16107) that Morris (1954) referred to *Viverravus gracilis* is much closer to *V. lutosus*. Both  $P_4$  and  $M_1$  in the Princeton specimen have the same overall dimensions as these teeth in the type of *V. lutosus* and seem identical to them, but the alveolus for  $P_3$  appears to be slightly longer. Matthew's (1909, p. 361) measurements of the type of Bridger *V. gracilis* suggest that the lower carnassial was relatively much broader than in the Cathedral Bluffs jaw.

**VIVERRAUS, cf. DAWKINSIANUS** (Cope)

A second and larger species than *Viverravus lutosus* in the New Fork fauna is indicated by portions of a lower jaw with only  $M_2$  preserved (U.S.N.M. No. 22467). The tooth is undoubtedly viverravid but its size and that of the more forward alveoli is decidedly greater than in *V. lutosus*. In this respect it is near *V. dawkinsianus*, to which it may be referred. However, it differs from that species, so far as can be determined, only in the depth of the lower jaw. The jaw is a little more robust than in *V. lutosus* but is not as deep as in typical Lost Cabin *V. dawkinsianus*.

**UINTACYON ASODES** Gazin

(Plate 7, figures 6 and 8)

While no new materials of *Uintacyon asodes* have been found in the La Barge horizon, a comparatively robust jaw that may be referred to this species was found in the New Fork tongue. The specimen (U.S.N.M. No. 22468; pl. 7, fig. 6) includes  $P_2$  and  $P_4$  to  $M_2$  inclusive. The carnassial is a little wider, but  $P_2$  is more reduced, as may be inferred from the better spacing of the roots of this tooth in the type. The large size of the molars that characterizes *U. asodes* in comparison with *Uintacyon massetericus* is further demonstrated

in  $M_2$  of the New Fork specimen. Measurements of teeth in the two Wasatch specimens are given below, together with those for the type of *U. massetericus*.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN SPECIMENS OF <i>Uintacyon</i>			
<i>U. massetericus</i>		<i>U. asodes</i>	
	A.M. No. 4250 Type	U.S.N.M. No. 19351 Type	U.S.N.M. No. 22468
$P_4$ , anteroposterior diameter:			
transverse diameter .....	6.0:2.9	6.1:3.3	5.8:3.5
$M_1$ , anteroposterior diameter:			
transverse diameter .....	6.9:4.8	7.5:5.5	7.9:5.9
$M_2$ , anteroposterior diameter:			
transverse diameter .....	4.2:3.6		6.0:5.1

**MIACIS, near *M. EXIGUUS* Matthew**

Included among the more recent collections made from the New Fork tongue is a lower jaw fragment with  $M_2$  and most of  $M_1$  (U.S.N.M. No. 22469), clearly of *Miacis* but representing a species distinctly smaller than *M. latidens*. In size it cannot be distinguished from *Miacis exiguus*, although all the heretofore described materials of this species have been recorded only from Gray Bull levels. The only feature seen in the two teeth that might be regarded as distinctive is a more forward position of the paraconid of  $M_2$ . This was noted in comparison with La Barge materials of *M.*, cf. *latidens* as well as with Gray Bull specimens of *M. exiguus*.

An isolated lower carnassial in the La Barge collection, too small to be included in *Miacis latidens*, may represent the same species as that present in the New Fork fauna. The form of its talonid, however, more closely resembles that of the other, much larger La Barge specimens.

**MIACIS, cf. *LATIDENS* Matthew**

(Plate 8, figure 1)

The miacid jaws (U.S.N.M. No. 19335) described in 1952 and tentatively referred to Matthew's Lost Cabin species *Miacis*, cf. *latidens*, exhibit a well-preserved and nearly complete cheek tooth series on the left side, illustration of which is included in this report. No further materials that may represent this species have been encountered.



**Cf. VULPAVUS AUSTRALIS Matthew**

(Plate 8, figure 5)

A single upper molar (U.S.N.M. No. 22474), much larger than in the Bitter Creek maxilla thought to be of *Vulpavus*, was found in association with *Heptodon* high on the slope of Fossil Butte. The tooth is rather close in size to  $M^1$  in the Gray Bull specimen (A.M. No. 16954) referred to *V. australis*. The protoconule, however, is a little less lingual and the cingulum is not as heavy. A slight mesostyle on No. 22474 cannot be determined for  $M^1$  of No. 16954 because of slight damage to this portion of the tooth, but it is lacking in  $M^2$  of the Gray Bull specimen.

**VULPAVUS ASIUS Gazin**

(Plate 8, figures 2 and 3)

Three additional specimens of *Vulpavus asius* bring the total to 11 that now represent this species in the La Barge fauna. One of these (U.S.N.M. No. 22470), a lower jaw including the first two molars, was collected by Privrasky west of Big Piney. The other two are isolated  $M_2$ 's from 12 miles north of Big Piney. Mention should also be made of an incomplete lower molar, surely of this species, from approximately 150 feet beneath the Tipton tongue about 13 miles north of Baggs, Wyo., one of the more productive localities for material of the Dad fauna.

A somewhat larger mutant, evidently of *Vulpavus asius*, is represented by four specimens from the New Fork tongue. One of these, U.S.N.M. No. 22471, includes both rami of the mandible and representation of  $P_4$ - $M_2$ . A composite of the teeth from both sides is shown for the left ramus in plate 8 (fig. 2) in comparison with the type (fig. 3) from the La Barge faunal level 12 miles north of Big Piney. The teeth in No. 22471 are among the larger for the New Fork mutant, which average a little larger than in the La Barge form. The observed ranges in size, however, do overlap. The depth of the jaw in No. 22471 is about the same as in the La Barge type.

The New Fork mutant makes a close approach in size to contemporary Lost Cabin *Vulpavus canavus* as represented, for example, by the comparatively small type specimen of *V. brevirostris* (Cope), and the lengths of the lower molars in No. 22471 can be nearly matched in certain of the Wind River specimens.  $P_4$ , however, is distinctly smaller and all the teeth are relatively narrower. The New Fork materials might have been allocated to *V. canavus* but they are



closer to *V. asius*, geographically as well as in form, so that it seems preferable to regard them as a progressive mutant of *V. asius*. Their stratigraphic position, of course, precludes regarding them in an ancestral relationship to *V. canavus*.

**Cf. VULPAVUS, sp.**

(Plate 8, figure 4)

A right maxillary fragment with  $M^1$  and  $M^2$ , U.S.N.M. No. 22473, from Bitter Creek closely resembles in the form of the two molar teeth a specimen of *Vulpavus australis* (A.M. No. 16954) from the Bighorn Basin but is distinctly smaller, and the inner cingulum, though worn, appears a little weaker. Matthew did not discuss or figure upper teeth of *Vulpavus* but it would appear from these teeth that there is somewhat less disparity in size between  $M^1$  and  $M^2$  and possibly the external shelflike cingulum is not as expanded as in *Miacis*.

**VASSACYON, cf. PROMICRODON (Wortman)**

A portion of the left ramus of a mandible, U.S.N.M. No. 22451, from the Gray Bull horizons southwest of Elk Mountain in the Fossil Basin represents beyond doubt, Matthew's genus *Vassacyon*. Only  $P_4$  and the talonid portion of the lower carnassial are included, but these together with alveoli for other molars correspond closely in size to Gray Bull *V. promicrodon*. The distinguishing feature in this specimen, demonstrating that it represents *Vassacyon*, is seen in the molar talonid. The heel of  $M_1$ , though having a well-defined lingual basin, has a comparatively high median crest. The basin is not as large and broad as in *Miacis* or *Vulpavus* and the crest is more trenchant. The median crest suggests *Uintacyon*, but this is denied by the much better-defined basin. Moreover, the jaw is relatively deep and robust as in *Vassacyon promicrodon*.

**CONDYLARTHRA**

**HYOPSODONTIDAE**

**HAPLOMYLUS SPEIRIANUS (Cope)**

(Plate 9, figures 1-4)

*Haplomylus speirianus*, as pointed out by Matthew (1915b, p. 314), is characteristic of the lower part of the Gray Bull and has not been found in the upper Gray Bull, Lysite, or Lost Cabin beds. This species is now recognized in the materials from several localities in the lower part of the Knight sequence. In addition to isolated upper and lower

teeth, there is a maxilla with  $M^1$  and  $M^2$  (Y.P.M. No. 14077; see pl. 9, fig. 1) from Bitter Creek that can be closely matched in Gray Bull materials from the Bighorn Basin. Lower jaws (U.S.N.M. Nos. 22429 and 22427; see pl. 9, figs. 2, 4) from the Knight exposures at the base of the escarpment west of Elk Mountain in the Fossil Basin have anterior molars comparable to those in larger Gray Bull materials, but  $M_2$  in both is actually and relatively smaller than in all but one of the U.S.N.M. jaws from the Gray Bull with this tooth preserved. A lower jaw with  $P_4$  and  $M_1$  (U.S.N.M. No. 22428; see pl. 9, fig. 3) from the Red Desert locality east of Steamboat Mountain can also be matched in Gray Bull specimens, but only among those having the smallest teeth.

There is considerable variation in tooth size in various Gray Bull materials referred to *Haplomylus speirianus*. Simpson (1937, p. 22), however, has shown that the materials from the Sand Coulee or lowest Wasatchian levels average distinctly smaller than those from the Gray Bull proper, although there is an overlapping in range. Teeth decidedly smaller than any of those in the National Museum Gray Bull sample were found very low in the Knight at a locality southeast of the Rock Springs uplift, approximately 20 miles southwest of Bitter Creek Station, by Henry W. Roehler of the Mountain Fuel and Supply Co. This must surely be the Sand Coulee level.

#### HYOPSODUS LOOMISI McKenna

(Plate 9, figures 5-7)

The species *Hyopsodus loomisi* as proposed by McKenna would appear to be a substitution for *Hyopsodus simplex* to include much that had been attributed to that species but which was not determinable in a lower jaw, or not actually distinctive of the type specimen. Most of the characters attributed to *Hyopsodus simplex* are highly variable throughout the lower Eocene but appear more consistently evident in the earliest Gray Bull specimens. The characters selected by McKenna as diagnostic for *H. loomisi* include the weakness of the hypocone and near absence of an external cingulum of the upper molars, which when coupled with small size would seem indicative of a distinct species, or at least of a primitive mutant of the Gray-bullian form referred to *H. miticulus*.

Several very small jaws in the Bitter Creek collection are believed to be this species, but only one upper molar conforms to the description. Other Bitter Creek maxillae show better development of the hypocone and external cingulum. Among the very small lower jaws

I note that although the paraconid is persistent on  $M_1$  and occasionally on  $M_2$ , the entostylid is rather variable. The presence of an entostylid would not seem to be necessarily an advanced character, because, although it is rather common in the Bighorn Gray Bull materials, it is usually weak or absent in the La Barge Knight specimens.

An isolated upper molar from the Red Desert locality east of Steamboat Mountain may also be referred to *Hyopsodus loomisi*, but the species does not seem to be represented in the Fossil Basin collections from west of Elk Mountain.

#### HYOPSODUS, cf. MITICULUS (Cope)

Jaws, maxillae, and isolated teeth that may be referred tentatively to *Hyopsodus miticulus* are included in the collections from the horizons of lower Gray Bull equivalence in the Knight. Reference of these, however, to the geographically remote New Mexican species may be questionable. Most of the material represents relatively small individuals, corresponding to about the lowest part of the size range determined for Gray Bull materials referred to this species. However, the largest individual represented in the Bitter Creek sample (Y.P.M. No. 14052) is just under the mean for the Gray Bull. Some that seem not referable to *H. loomisi* are smaller than any in the U.S.N.M. Gray Bull sample, but it should be noted that the latter does not include Sand Coulee *Hyopsodus* material.

To *Hyopsodus miticulus* are also referred specimens from the Lysite equivalent in the Fossil Basin, materials that might otherwise have been identified as *Hyopsodus lysitensis* or *Hyopsodus mentalis lysitensis*. In a statistical study of *Hyopsodus*, currently under way, I find that the range of measurements for specimens of the smaller form, generally designated *H. m. lysitensis*, in the American Museum and Princeton University collections from the Cottonwood Draw Lysite, corresponds very well and is included within that for the *H. miticulus* materials from the Gray Bull. I am unable to justify a distinction on size or progressiveness. The frequency distribution for size of teeth in *Hyopsodus mentalis* in a small sample from the Largo beds of New Mexico is discordant with that for the Lysite materials, although Van Houten (1945, p. 434) and Simpson (1948, p. 383) have thought that that Largo may be more nearly Lysite than Lost Cabin in age. I do not think that the Lysite *Hyopsodus*, if contemporaneous, is the same species as that recorded for the Largo.



**HYOPSODUS WORTMANI Osborn**

Ten more specimens of *Hyopsodus wortmani* encountered in later collections representing the La Barge fauna brings the total for this species up to about 39, much less abundant than *H.*, cf. *mentalis*. Later collections from the New Fork horizon, however, show that *H. wortmani* there outnumbers the larger form about 10 to 6 in the small sample at hand. A single specimen, U.S.N.M. No. 22660, from the collections of the Dad fauna is referred to this species; all the remaining specimens from the exposures beneath the Tipton tongue south of Dad, Wyo., are of the very large species *H. browni* and *H. walcottianus*.

**HYOPSODUS, cf. MENTALIS (Cope)**

Reference of Lostcabinian materials of *Hyopsodus* to the species *H. mentalis*, while recognizing *H. miticulus* as the name for Gray Bull materials, may well be perpetuating a taxonomic error. It is not improbable that the Wyoming sequence of the forms concerned is evolution in situ, whereas *H. miticulus* and *H. mentalis* are reported to be contemporary in the Almagre of New Mexico, although only *H. mentalis* seems persistent into the Largo beds, according to Matthew's interpretation of the distribution of these species.

Some 70 or more specimens of *Hyopsodus* in the collections representing the La Barge fauna are considered as possibly representing *H. mentalis*, bringing the total for this locality to approximately 146. Not previously recognized in the New Fork fauna, six specimens or about a third of the *Hyopsodus* material from above the Tipton tongue in the La Barge-Big Piney area may also be included in this species. It is interesting to note, however, that of the materials I have seen, none of the specimens representing *Hyopsodus* in the Dad fauna, appears to be in this size range, although the horizon surely corresponds closely in age to that of the La Barge fauna.

**HYOPSODUS BROWNI Loomis**

The species indicated here is the same as that for which Kelley and Wood (1954, p. 355) have used the name *Hyopsodus powellianus*. Unfortunately, the type of *H. powellianus* is from an unknown horizon in the Bighorn Basin, and while it may well have come from the Lysite horizon, it could also be from the Lost Cabin level and represent a small individual of the form Matthew has called *H. walcottianus*. *Hyopsodus lemoinianus* also has for its type a specimen from an unknown horizon in the Bighorn Basin. *H. lemoinianus* has pri-



ority over *H. powellianus*, and while Matthew placed it in synonymy with *H. mentalis*, it seems to be nearly or quite outside the observed range for this species in the Wind River Lost Cabin and at about the upper limit in the La Barge fauna. It certainly falls near the mean for the Cottonwood Draw Lysite specimens called *H. powellianus*. Nevertheless, in view of the possible confusion at certain levels, probably *H. browni* is the least questionable designation.

In addition to the specimens from near Knight Station in the Fossil Basin that were described as belonging to this species in 1952, I refer also a maxilla with part of  $M^2$  and  $M^3$  from high on the southwest slope of Fossil Butte, in the deeper red beds just beneath the Green River, and a lower jaw with  $M_2$  and part of  $M_3$  from the saddle on the north side of Fossil Butte in the Fossil Basin.

This large species is evidently not represented in the rather abundant *Hyopsodus* specimens from below the Fontenelle or Tipton tongue in the La Barge-Big Piney area. A single specimen (U.S.N.M. No. 22667), however, collected by N. C. Privrasky of the U. S. Geological Survey, from a locality he regarded as near the base of the Knight in this area, is much larger than any of the *Hyopsodus*, cf. *mentalis* material and may tentatively be referred to *H. browni*. In the Dad fauna, on the other hand, associated with *Lambdaotherium*, most of the specimens of *Hyopsodus* at hand conform to the size range of *H. browni*. The remaining specimens are quite outside the range and may be included in small *H. wortmani* or very large *H. walcottianus*. Also, above the Tipton tongue of this area, in the Cathedral Bluffs member, Morris (1954, p. 197) has listed *Hyopsodus paulus*. These specimens, consisting of a  $P^4$ , an upper molar, and an  $M_3$  are of a larger species than *H. paulus* and may tentatively be referred also to *H. browni*. Their size would not warrant recognizing *H. walcottianus* in the Cathedral Bluffs fauna.

#### HYOPSODUS, cf. WALCOTTIANUS Matthew

Material from the Knight beds that may appropriately be referred to very large, but rare, *Hyopsodus walcottianus* has been found at localities near Dad, Wyo. A lower jaw with incomplete  $M_2$  and  $M_3$  (U.S.N.M. No. 22663), a maxilla with  $M^1$  and  $M^2$  (U. of Calif. No. 43592) and an isolated  $M^1$  in the National Museum collection from the Knight beneath the Tipton tongue along the escarpment south of Dad appear much too large to be included with the contemporary materials regarded as representing *H. browni*. Also, a single lower jaw with  $P_4$  and  $M_1$  (U.S.N.M. No. 22669) from the New Fork

seems large enough to be included in this species. Matthew in 1915 (b, p. 326) noted only three specimens of *H. walcottianus*, including the type in the collection from the Lost Cabin beds of the Wind River Basin and two from this horizon in the Bighorn Basin.

## PHENACODONTIDAE

### PHENACODUS PRIMAEVUS Cope

The absence of *Phenacodus* in the abundantly represented La Barge fauna of the Knight was earlier (1952) noted, although the type of *P. primaevus* is from a somewhat earlier horizon along Bear River near Evanston. A well-worn  $P_4$  and lower molar (U.S.N.M. No. 22668), evidently associated, from the Bitter Creek locality compare very closely in size with Gray Bull materials referred to *Phenacodus primaevus*. The lower molar is worn so that its pattern is poorly revealed. The premolar, however, is clearly of *Phenacodus* and can be matched in detail with this tooth in *P. primaevus*, although the posterointernal angle or entoconid portion is broken away.

The lower jaw of *Phenacodus* described in 1952 (p. 61) as coming from beneath the variegated deposits of the Knight about 3 miles east of Fossil Station is now known to be from the Evanston formation (Gazin, 1956b).

### PHENACODUS, cf. VORTMANI (Cope)

(Plate 9, figures 8 and 9)

A maxilla with  $P^4-M^2$  and a lower jaw with  $P_3-M_3$ , together with other tooth portions belonging to the same individual, representing a small species of *Phenacodus*, were found at a locality to the southwest of Elk Mountain in the Fossil Basin. It is not certain, however, that the horizon represented is as low as the Gray Bull level at the base of the escarpment due west of Elk Mountain. The localities are a couple of miles apart.

The size of the species represented is comparable to *Phenacodus vortmani*, or possibly to *P. copei*. The details of  $P_3$  and  $P_4$  correspond more closely to the description given by Granger (1915, p. 343) for *P. vortmani*, although the horizon represented by the Fossil Basin specimen is in all probability not as late as that for the type. It should be noted, however, that Granger recognized *P. vortmani* in all three levels of Wasatchian time.

### PHENACODUS, cf. BRACHYPTERNUS Cope

A single upper molar in the collection from the Red Desert locality east of Steamboat Mountain is about the size of an  $M^1$  in *Ectocion*

*osbornianum*, but evidently does not represent this genus. The cusps are lower and more bunodont and there is much less indication of transverse lophs. Moreover, the enamel is perhaps a little more rugose. Although the more characteristic  $P_4$  of *Phenacodus brachypternus* is not included in the material, it seems probable, nevertheless, that this small species is represented rather than somewhat larger *P. vortmani* or *P. copei*.

## MENISCOTHERIIDAE

### MENISCOTHERIUM, cf. PRISCUM Granger

(Plate 10, figures 5 and 6)

A small species of *Meniscotherium* in the Bitter Creek fauna is represented by about six specimens. Although the type of *M. priscum* from the Clark Fork beds could not be located in the American Museum collections, the dimensions of the teeth given by Granger (1915, p. 360) are closely comparable to those in the Bitter Creek specimens. Their size is only slightly greater than in the New Mexican form *M. tapiacitis* Cope, but, as noted by Granger, the metastylid of the lower molars is much more prominent in the Wyoming material.

In a comparison of upper cheek teeth in a maxilla from Bitter Creek (see pl. 10, fig. 5) with upper dentitions from later horizons of the Wasatch, it is noted that in addition to smaller size the teeth are relatively short (anteroposteriorly) and broad. The extended lingual portion in each also seems anteroposteriorly compressed.

Isolated teeth of distinctly small size from the Red Desert locality are also referred to this species. Moreover, fossil materials collected by Henry W. Roehler near the base of the Knight sequence at localities on the western and southeastern flanks of the Rock Springs uplift include isolated teeth of this species in association with *Haplomylus speirianus*. The faunal levels represented are about comparable to those at Bitter Creek.

Some very fragmentary material, but including one complete lower molar, of a small *Meniscotherium* was found low on the south-facing escarpment to the west of the saddle north of Fossil Butte. The tooth is almost identical in size with  $M_2$  in the lower jaw (U.S.N.M. No. 22432; pl. 10, fig. 6) from Bitter Creek. The presence of *Meniscotherium* so close in size to *M. priscum* on the slopes on the opposite side of the ravine to the northwest of Fossil Butte is rather indicative of a lower Gray Bull level in this area, lower than the Wasatchian horizon represented in the saddle which has produced remains of *Meniscotherium* more nearly comparable to *M. robustum*.



**MENISCOTHERIUM ROBUSTUM Thorpe**

(Plate 10, figures 1 and 2)

The distribution of *Meniscotherium robustum* would appear to be characteristic of the upper part of the Knight formation beneath the Tipton tongue and to be nearly limited to the Green River Basin of Wyoming. Its area of greatest abundance is the vicinity of La Barge and Big Piney, but it has been found near Tipton Butte, and to the southeast of the Rock Springs uplift as well as on its western flank. Also, a maxilla and a portion of a lower jaw, which may represent this species or a form near it, were found in the adjacent Fossil Basin at localities high in the Knight beneath the Green River beds on Fossil Butte. Besides these, maxillae and a jaw portion belonging together were discovered in association with a considerable amount of *Coryphodon* material on the escarpment to the west of Elk Mountain. Distribution of the species, however, does not appear to have extended as far east as the Muddy Creek area on the east side of the Washakie Basin. No material of *Meniscotherium* has been observed in any of the several collections from beds beneath the Tipton tongue in the vicinity of Dad and Baggs, Wyo., and this species has not been reported from either the Wind River or Bighorn Basins.

While the vertical range of *Meniscotherium robustum* is limited upward, as far as known, by the Fontenelle or Tipton tongue of the Green River, its distribution downward remains somewhat uncertain. It may well characterize only the Lostcabinian level but if it evolved in situ from the early Graybullian *M.*, cf. *priscum*, of the area, the Lysitean stage of this development has not been clearly demonstrated in the Green River Basin. It is entirely possible that the Fossil Butte specimens which seem near *M. robustum* represent this age. The teeth in the maxilla (U.S.N.M. No. 22670) are larger than in the New Fork *M.*, cf. *chamense*, but are at about the lower limit of the observed range in size for *M. robustum*. Only two maxillae in the La Barge collection have teeth as small. The lower jaw fragment (U.S.N.M. No. 22794) has  $P_3$  and  $P_4$  only slightly larger than in the *M.*, cf. *chamense*, material but the jaw itself is about as robust as in *M. robustum*. It is interesting to note, however, that the specimen from the Fossil Basin locality west of Elk Mountain (U.S.N.M. No. 22795), evidently a Gray Bull level, has teeth fully as large as in *M. robustum*. There is no association here with *M. priscum*, however. Presumably the horizon is not as early as that at Bitter Creek.



**MENISCOTHERIUM, cf. CHAMENSE** Cope

(Plate 10, figures 3 and 4)

As noted for the La Barge horizon, remains of *Meniscotherium* are found to be exceedingly abundant in the New Fork collections. More than 120 specimens have been added to the 3 reported in 1952, a few of which are beautifully preserved skulls. Partial skeletons are also included in certain instances. Unlike the New Mexican collections, the New Fork materials are surprisingly uniform in size, corresponding very closely in tooth proportions to the type of *Meniscotherium chamense*. Moreover, the range in size of teeth does not appear to overlap that of larger and earlier *Meniscotherium robustum*. Except for the persistent size and age difference there is surprisingly little to distinguish the two species in the Big Piney area. There is a suggestion, however, that the smaller and later form referred to *M. chamense* shows a somewhat less progressive P<sup>3</sup>. The talon of this tooth in certain specimens seems simpler with less development of the accessory cuspules.

I do not think that the New Fork species is derived from *M. robustum* in the underlying beds. It is more reasonable to suppose that *M. robustum* was supplanted by the smaller form as a migrant from elsewhere, presumably New Mexico. An excellent specimen obtained by Princeton University (P.U. No. 14875) from Lost Cabin beds north of Moneta in the Wind River Basin compares closely with the type of *M. chamense*, supporting Granger's conclusion that this species is present also in the typical Lost Cabin beds, but his inference from this that the Largo beds are of Lost Cabin age may not follow.

With the relative abundance of *Meniscotherium* in the New Fork fauna it is important to note that no representation of this genus has been found in the Cathedral Bluffs exposures of the Washakie Basin. Morris (1954, p. 199) has used this as evidence supporting a later age for the type Cathedral Bluffs. It seems more than likely, however, that the absence is of ecologic significance rather than necessarily implying later time, inasmuch as *Meniscotherium*, as noted in the preceding discussion, is also missing from the Dad fauna of the underlying beds of the same area, as well as from the nearby and still earlier Four Mile fauna of McKenna.

PANTODONTA  
CORYPHODONTIDAE  
**CORYPHODON RADIANS** (Cope)

(Plate 11, figures 1-5; plate 12, figures 1 and 2)

*Coryphodon* would appear to be most abundantly distributed in the lower levels of the Knight. Remains are of common occurrence at the Bitter Creek locality and at the base of the Knight section west of Elk Mountain in the Fossil Basin. Much highly fragmentary material was noted along the lower slopes of Fossil Butte although the precise level represented here is not certain. Remains are much less frequently encountered in the higher levels in the La Barge-Big Piney area and none has been found in the New Fork and Cathedral Bluffs beds. Extinction may well have coincided with the changes that brought about the Tipton tongue of the Green River.

*Coryphodon radians* is the first name that has been applied to *Coryphodon* in North America; and since the type material is from the Bear River locality near Evanston, there is no question of its being represented in the Knight in at least one of the faunas for this member. In all probability all the reported materials from the different horizons of the Knight are of this species. However, only one of the skulls in our collection, U.S.N.M. No. 20737 (see pl. 11, fig. 1) from near La Barge shows the spur from the metacone described by Osborn (1898, p. 213) as characterizing *C. radians*. I suspect, however, that this is, as a vestigial feature, highly variable. I note also that the spur extending posteroexternally from the protocone to the posterior cingulum of this tooth must be regarded as variable, because in a skull from Bitter Creek (U.S.N.M. No. 22745; pl. 11, fig. 4) it is exhibited on the right side but not the left.

Two skulls (U.S.N.M. Nos. 22745 and 22748; pl. 11, figs. 4, 5) and an incomplete pair of lower jaws (U.S.N.M. No. 22746, pl. 12, fig. 2) from Bitter Creek could with certainty be referred to Cope's *Coryphodon armatus*. There is no doubt but that this is the place where he obtained the remains of two poorly preserved skulls upon which the species was based. *C. armatus* was the third North American species to be named, and the second, *C. semicinctus*, was placed in synonymy with *C. radians* by Cope himself. *C. armatus* was the type of Cope's genus *Metalophodon* characterized by the unusual appearance of  $M^2$ . Earle (1892) regarded *Metalophodon* invalid because of variation in the characters of  $M^2$ . I believe, however, that the tooth in this position, as figured by Cope in his Tertiary Vertebrata (1884, pl. 49, fig. 1),

is an  $M^3$  from another individual. The difference between the two  $M^3$ 's is then a matter of wear and of individual variation. The extent of the difference between them with respect to the posterior spur from the protocone was observed between two sides of the same skull as mentioned above.

The pair of jaws from Bitter Creek (U.S.N.M. No. 22746) includes the three molars.  $M_3$ , as in the tooth so identified by Cope (pl. 49, fig. 6) has the posterior crest parallel to the anterior. This condition is quite like that in the lower jaw regarded as associated with the type of *C. radians* (Cope's pl. 46, fig. 2). Lower jaws with a skull (U.S.N.M. No. 21026) from the Gray Bull horizon at the base of the escarpment west of Elk Mountain in the Fossil Basin also show (see pl. 12, fig. 1) this type of  $M_3$ . None of the Knight lower jaw material so far observed exhibits the so highly divergent or V-shaped posterior crest characterizing the genotype *C. cocaenus*, and that is comparatively common in Bighorn Basin specimens. The *C. cocaenus* condition exhibited by the Bighorn Basin specimens would appear to be primitive, and more like the Paleocene pantodonts, as pointed out to me by Dr. Elwyn Simons, although the form representing this condition in the Gray Bull fauna of the Bighorn Basin cannot, of course, be ancestral to that at Bitter Creek. Dr. Simons has undertaken a study of *Coryphodon* as a sequel to his study of Paleocene pantodonts, and his much-to-be desired revision of the numerous species of *Coryphodon* and his conclusions on their relationships is eagerly awaited.

## DINOCERATA

### UINTATHERIIDAE

#### Cf. *BATHYOPSIS FISSIDENS* Cope

Further excavation in 1953 at the locality where jaws described as probably representing *Bathyopsis fissidens* (U.S.N.M. No. 19990) were found has yielded considerably more skeletal material. The bone is rather badly shattered but careful preparation has saved about nine presacral vertebrae, including the atlas and axis, together with the sacrum and several rib portions. Representing the forelimbs is the distal part of a humerus, both radii, the greater part of both ulnae, and three carpals. The hindlimbs are represented by the head and condyle of a femur, patellae, a nearly complete tibia, almost all of the right tarsus, and the third metatarsal.

The limb material for the most part is rather flattened by crushing,



although the foot bones, of denser material, have retained much of their original shape. The skeletal portions closely resemble those in Bridger *Uintatherium*. The limb bones, though about two-thirds the length of those in an upper Bridger animal, are relatively much more slender. In comparison with the skeletal material Dorr (1958) has called *Prouintatherium*, I note that the groove between the inner and outer or trochlear and capitellar portions of the distal articular surface of the humerus is more obtuse, approaching *Uintatherium* in this respect. Also, the olecranon of the ulna curves backward more and the sigmoid notch faces more proximally, as in *Uintatherium*.

The astragalus figured by Dorr belongs to *Coryphodon*, as he suspected. The New Fork astragalus is much like that in *Uintatherium* but shows a somewhat less flattened surface for the tibia, and that for the cuboid and navicular is relatively a little deeper in a dorso-plantar direction and not so wide. The latter surface, moreover, is sharply tilted with respect to the tibial surface and they approach one another at a high angle. In *Uintatherium* these surfaces of the astragalus are more nearly opposite one another. This suggests greater forward tilting of the tibia with respect to the metatarsal direction. An additional feature noted is that an astragalar foramen is not enclosed or completed in the New Fork animal, whereas formation of the foramen seems characteristic of the Bridger animal.

## PERISSODACTYLA

### EQUIDAE

#### HYRACOTHERIUM, cf. *ANGUSTIDENS* (Cope)

(Plate 13, figure 3)

In assigning the Bitter Creek material of *Hyracotherium* tentatively to *H. angustidens*, I have followed Kitts in his belief that the materials from Graybullian beds in both New Mexico and Wyoming represent a definably more primitive stage in this genus than the later Wasatchian specimens. This is without regard for the rather striking range in size observed. Some teeth are as large as any referred to *H. vasaccense* in the La Barge collection and others are smaller than any that I had previously referred to *H. index*. No statistical treatment of this material seemed feasible, as all but about four specimens of the approximately three dozen consist of isolated teeth from various positions.

Three of the isolated teeth are believed to be P<sup>3</sup>, as determined from their somewhat less transverse diameter in comparison with their



length than in  $P^4$ . In these the primary cusp and tritocone (paracone and metacone) are less widely separated than in  $P^4$ , or than in  $P^3$  of later forms. In each the protoloph extending toward the parastyle is not appreciably deflected anterolingually, but shows a distinct enlargement representing the protoconule, certainly more discernable than in the specimen figured by Kitts (1956, fig. 5) for this species. All these, moreover, are of a size commensurate with the smaller La Barge specimens earlier referred to *H. index*. I suspect that there is a considerable amount of variation in the development and position of the protoconule of  $P^3$  in any population of *Hyracotherium* and I have attempted to illustrate this in plate 13 where the specimens in figures 4 to 9 inclusive show increasing significance of the protoconule in the La Barge material of *H. vasacciense*.

It seems more than likely that the comparatively advanced lower Knight form represented at Bitter Creek gave rise to typical *H. vasacciense* of the later Knight beds, possibly in a dichotomous arrangement, such as seems indicated in the La Barge materials (see Kitts, 1956, p. 49; and Gazin, 1952, p. 65) other than those now referred to *H. craspedotum*.

Marsh's type of *Eohippus pernix* is from the Bitter Creek locality. This name was regarded by Kitts as a synonym of *Hyracotherium vasacciense*. It is possible that this interpretation is correct, but it seems more than likely, in the absence of published information to the contrary, that he regarded the Bitter Creek fauna as later than it is.

A few isolated teeth from the Red Desert locality and about 24 specimens from the Lower Wasatchian or Gray Bull level to the west of Elk Mountain in Fossil Basin are also referred tentatively to *H. angustidens*. The latter show a range in size as great as that at Bitter Creek but with a somewhat greater average size. A single maxillary portion exhibits  $P^3$  and  $P^4$  (pl. 13, fig. 3) and these teeth more nearly approximate the nonmolariform condition cited by Kitts for this species.

#### HYRACOTHERIUM VASACCIENSE (Cope)

Plate 13, figures 1, 2, 4-10)

As revised by Kitts, *Hyracotherium vasacciense* includes among its synonyms *Hyracotherium index*, the second and smaller of the two species described by Cope from the Knight beds of Fossil Basin. Although I have shown that for the La Barge collection  $M_2$ , excluding the very large specimens, is clearly bimodal in its proportions, and Kitts (1956, p. 52) has found the same to be true for  $M_3$ , the evidence

for this in the more limited and generally more fragmentary remains of *Hyracotherium* at other horizons and localities in the Wasatch is not so easily demonstrated. I am convinced that two forms are represented in the rather striking size range for Wasatch materials now allocated to *H. vasacciense*, but there is the practical matter of separating them in horizons other than at La Barge or Dad (Kitts, 1956, p. 49), because the modes thus postulated would no doubt shift with time. It may be noted that in the smaller as well as the larger of the two La Barge forms included under *H. vasacciense* P<sup>3</sup> is progressive, as Kitts has defined this species. In plate 13, figures 4 and 9 might be interpreted as representing the smaller form.

Nearly 200 specimens from the La Barge horizon in Sublette County are now referred to *H. vasacciense*. Of this number more than a third are in a size range that was earlier included under *H. index*. The smaller specimens are relatively fewer in the Dad fauna, and in the New Fork only 2 of the 33 specimens of *Hyracotherium* are small enough to have been included in *H. index*. However, 10 out of this total are thought, for the most part on the basis of size, to represent *H. craspedotum*. A shift in modes for the New Fork species may also be involved. A somewhat different distribution is noted for the Cathedral Bluffs although only five specimens are known. Three of these are of a size that would have included them with *H. index*. The other two are referred to *H. craspedotum*. Incidentally, none has characters that would justify their inclusion in *Orohippus*. The upper molar associated with P.U. No. 16111 shows no evidence of a mesostyle.

#### HYRACOTHERIUM, cf. CRASPEDOTUM Cope

(Plate 13, figure 11)

Essentially, the specimens from the Knight that I had tentatively assigned to *Hyracotherium venticolum* are those which Kitts (1956, p. 53) regards as representing *H. craspedotum*. These are for the most part strikingly large specimens, but rather few in number, that seemed beyond the limit for *H. vasacciense*. In two instances, however, maxillary portions are known in which P<sup>3</sup> is of the type described by Kitts as characterizing *H. craspedotum*. One of these, P.U. No. 16173, from Fossil Butte was particularly mentioned by both Kitts (1956, p. 53) and me (as *H. venticolum*, 1956, p. 66); and the other is from the Cathedral Bluffs (U.S.N.M. No. 22497; see pl. 13, fig. 11). A second specimen from Cathedral Bluffs is a lower jaw (P.U. field No. 326W) in which the combined length of M<sub>2</sub> and M<sub>3</sub> is

about 20.0 mm. The approximately 10 specimens from the New Fork are mostly isolated teeth of large size.

*Hyracotherium craspedotum* is evidently a contemporary of *H. vasacciense* but probably derived from earlier *H. angustidens*. *H. vasacciense*, however, may have originated in a somewhat more progressive form than typical *H. angustidens*, such as represented by the material from Bitter Creek. *H. craspedotum* most likely did not give rise to *Orohippus*.

## BRONTOTHERIIDAE

### LAMBDOOTHERIUM POPOAGICUM Cope

(Plate 12, figures 8 and 9)

In the later collecting at the La Barge and New Fork levels, remains of *Lambdaotherium* continued to be among the most frequently encountered. With the exception of a well-preserved pair of lower jaws (U.S.N.M. No. 22758) from the Muddy Creek locality 12 miles north of Big Piney, near where the earlier-described (1952, pl. 10) skull was found in 1949, much of the material consists of rather fragmentary jaws and isolated teeth. Some 30 or more specimens were added to the La Barge collection and something over 70 were found in the New Fork beds, which have received rather more attention in late years.

No material of *Lambdaotherium* has as yet been encountered in the rather sparsely fossiliferous Cathedral Bluffs beds in the Washakie Basin; however, at least 21 specimens referred to *L. popoagicum* have been seen in collections representing the Dad faunule from beneath the Tipton tongue in the same area. These are for the most part isolated teeth in the collections of Princeton University and the University of California, although in the Princeton collection there is a lower jaw (P.U. No. 16118) with three molars. A single specimen in the National Museum collection (No. 22759) exhibits  $P_4$  and  $M_1$ .

### BRONTOTHERIID, near PALAEOSYOPS FONTINALIS Cope

The Princeton University specimen (No. 16110) from the Cathedral Bluffs that Morris (1954) and I (1959) have listed as *Eotitanops*, sp., is a right maxillary fragment with  $Dp^3$ ,  $Dp^4$  and  $M^1$ . Comparison of the teeth with those in the type of *Palaeosyops fontinalis* (A.M. No. 5107) shows them to be quite similar and only slightly smaller. The length of the ectoloph portion of  $M^1$ , for example, measures 24.0 mm., whereas in the type this dimension is 26.2 mm. Also,  $M^1$



exhibits a small protoconule but no metaconule, as in the type. Whether this specimen should be referred to *Palaeosyops fontinalis* or regarded as a large species of *Eotitanops* is not determined. Although direct comparison is not feasible, M<sup>1</sup> in the Cathedral Bluffs specimen is only a little larger than would be required for good occlusion with the type lower jaw of *Eotitanops princeps*.

An additional specimen, U.S.N.M. No. 22766, that might also be referred to *P. fontinalis* but which is of a somewhat larger individual than the Princeton specimen was found very near the top of the red beds in the Oregon Buttes area, immediately to the southwest of Continental Peak and near its base. The red beds and the overlying greenish sequence here have been mapped as belonging to the Cathedral Bluffs member. The material consists of numerous bone fragments and portions of upper teeth, but with only P<sup>1</sup>-P<sup>3</sup> nearly complete and the lingual portions of P<sup>4</sup> and M<sup>1</sup> preserved.

The type of *Palaeosyops fontinalis* was found by Cope "on a bluff on Green River near the mouth of the Big Sandy Creek, Wyoming." Osborn considered the horizon represented as Bridger A, but I have some doubts as to the existence of a distinctive unit of true Bridger beneath that defined by Matthew as "B." The specimen may well have come from a sandy zone or lentil high in the Green River formation, as developed in the Bridger Basin. In any case there is suggestion of an approximate correlation with the upper part of the Cathedral Bluffs member in the Washakie Basin, inasmuch as the locality data for the Princeton specimen show it as coming from a horizon high beneath the Laney shale contact (sec. 4, T. 15 N., R. 93 W., evidently fossil loc. 1 on Morris's map, 1954, p. 198).

*Palaeosyops fontinalis* is not particularly close to typical Bridger *Palaeosyops*, as indicated by both Cope and Osborn. It is very much smaller than *P. paludosus*. As noted by Peter Robinson in his study of the Huerfano material, *Palaeosyops fontinalis* morphologically resembles *Eotitanops borealis*. *P. fontinalis* is in all probability an intermediate stage in a line of development from typical *Eotitanops* to *Palaeosyops*, as well as being intermediate in size between *E. borealis* and *P. paludosus*. Whether this stage should be referred to *Paleosyops* or *Eotitanops* seems a rather arbitrary matter. Since the Cathedral Bluffs fauna on other evidence should no doubt be regarded as Wasatchian rather than Bridgerian, one might be justified in allocating *P. fontinalis* to *Eotitanops*.



## ISECTOLOPHIDAE

## HOMOGALAX PRIMAEVUS (Wortman)

(Plate 12, figures 5 and 6)

Three species of *Homogalax* have been described on Wasatchian materials from the Bighorn Basin and all are about equal in size. In all probability these represent but a single species, although Wortman (1896) has attempted to distinguish between them on the basis of premolar characteristics. The earliest named, *Homogalax semihians* (Cope), was based on a specimen in which there is a small deutercone on  $P^2$  and said to have a diastema between  $P^1$  and  $P^2$ .  $P^1$  is missing but the alveoli are present to show that there was no diastema in this position. However, the molars in the type are badly worn and because the premolars seem relatively small there is no certainty that the specimen actually represents *Homogalax*. A revision of the tapiroids currently under way by Leonard Radinsky at Yale University may resolve this problem. The type of *Homogalax* was designated by Hay as *H. primaevus*—one of two species named by Wortman in 1896 and characterized as lacking a deutercone on  $P^2$ . The other, *H. protapirinus*, was characterized as possessing a strong deutercone on this tooth. I suspect that this cusp, nearly functionless in a position so far forward in the series, may well have been highly variable in development.

Seven specimens, consisting of maxillae, jaws, and separate teeth, from the Bitter Creek locality represent *Homogalax* and are comparable in size to the named Gray Bull species. None of the Bitter Creek specimens exhibits  $P^2$ , but U.S.N.M. No. 22767 (pl. 12, fig. 5) has comparatively well-developed deutercones on  $P^3$  and  $P^4$ , so that it would be reasonable to suppose that this cusp was also present on  $P^2$  in this individual.

## ISECTOLOPHID, near HOMOGALAX PRIMAEVUS (Wortman)

Among the materials of *Hyracotherium* and *Heptodon* encountered in the Knight exposures near Dad P. O. are remains of a small perissodactyl that cannot be assigned to either of these genera. About eight or nine specimens are included in the collections at hand and nearly all are from the large promontory of exposures beneath the Tipton tongue to the southwest of the State highway (330) bridge over Muddy Creek. Included are jaws, maxillae, and isolated teeth which represent a species about the size of the larger of the forms of *Hyracotherium* from here.

The very well-defined cross crests and more forward-directed crista obliqua of the lower molars, together with the elongate, uninterrupted transverse lophs of the upper molars, show that these specimens should not be included in *Hyracotherium*. Moreover, a maxillary fragment, U.S.N.M. No. 22788, with P<sup>3</sup> and P<sup>4</sup>, shows P<sup>3</sup> to be rather more like *Homogalax* than *Hyracotherium*. It exhibits a very prominent parastyle and the talon is constricted lingual to this. The deuterocone is very high and placed well forward with a high, more laterally directed protoloph which does not join the ectoloph. There is no crest to the tritocone. Kitts (1956) has noted the occasional absence of a crest between the deuterocone and tritocone in P<sup>3</sup> of *Hyracotherium craspedotum* but I do not believe these teeth would otherwise be confused.

The tapiroid upper molars are readily distinguished from *Heptodon* in the more buccally situated metacone, which is decidedly conical and externally ribbed. Moreover, M<sub>3</sub> has a particularly well-developed and somewhat basined hypoconulid portion. The crests of the molars, both uppers and lowers, are rather less elevated than in *Heptodon*.

A rather close correspondence is seen to Graybullian material of *Homogalax primaevus* but with specimens rather near the lower limit in size. The molars, however, are relatively a little lower crowned than in most of the *Homogalax* material examined. A close resemblance is also evident in comparisons with the much larger materials of Bridger *Parisectolophus*, but these later specimens show a relatively longer trigonid portion in the lower molars, with a tendency toward development of a basin approximating that of the talonid.

Heretofore *Homogalax* has been considered as indicative of Graybullian time but now there would appear to be little doubt but that this genus, or a closely related isctolophid, is present in beds of Lost Cabin age, in association with *Heptodon* and *Lambdotherium*. The encountering of such a form in these beds is, of course, not unexpected because of the continuity of this line into Bridgerian and Uintan time.

## HELALETIDAE

### HEPTODON VENTORUM (Cope)

(Plate 13, figure 12)

Nearly all of the La Barge tapiroid material can, on the basis of size, be regarded as typical *Heptodon ventorum*, although as previously noted (1952) most of these specimens have teeth a little smaller

than in the type, but the correspondence is closer than it is to the type of *H. calciculus*.

With regard to the New Fork materials of *Heptodon*, excluding a very small Dp<sup>4</sup>, the average size of teeth in some 20 specimens is distinctly larger, including specimens more nearly corresponding to the type of *H. posticus*. There is, nevertheless, an overlap in range with the La Barge suite. These New Fork materials are surely of a single species but, because of overlapping range, they should probably be regarded as representing a mutation in time. Possibly this could be cited as *H. ventorum* mut. *posticus*.

A similar situation, but with specimens of smaller average size than in the La Barge sample, is noted in the Fossil Basin collections considered as Lysitean in age. Material from the type Knight and from the distinctly reddish beds high beneath the Green River shale on Fossil Butte include the specimens cited in 1952 as *Heptodon ventorum*. Additional material from both localities, including an M<sub>3</sub> from Knight station and four lots of associated tooth fragments from Fossil Butte, corresponds more nearly to the *H. calciculus* type. Again the degree of difference involved here cannot be regarded as more than subspecific and represents a mutation in time. Nevertheless, in considering the upper and lower ranges represented, for example, by *H. ventorum calciculus* and *H. ventorum posticus*, a difference is involved that is surely of full species value. It appears, moreover, that we are faced with an association of these two in the New Fork horizon from which a single very small Dp<sup>4</sup> can scarcely be included with the material of *H. v. posticus*. A small tapiroid seems evident also in the Wasatchian (?) beds to the northwest of the Oregon Buttes, represented by a comparatively small jaw in which the molar teeth have lost most of their enamel. I suspect that Bridger *Helalestes* was derived from a small variant of *Heptodon* and not *H. v. posticus*.

A situation particularly difficult of interpretation is presented by the *Heptodon* materials from the Dad locality. The four specimens from here in the National Museum collections, known to have come from the same horizon, can readily be allocated to *Heptodon ventorum* (s.s.), much as in the case of the La Barge materials. One of these (U.S.N.M. No. 22498; pl. 13, fig. 12) is a well-preserved lower jaw which corresponds rather closely in length of tooth row to the type of *H. ventorum*, although the width of the teeth is a little less. Included in the University of California materials from the Dad area, however, are remains of an immature individual (No. 43703) which includes maxillae, jaws, and some fragmentary limb material of a



distinctly smaller form. Teeth from Dp2 to M2 of both upper and lower series are included and the lower molars are actually a little smaller than in the type of *H. calciculus*. Also in the U. of C. collection is an isolated upper molar of unusually large size. This, however, is described in field notes as coming from float along the base of the escarpment, so that its level is not known, except that it is likely from beneath the Tipton tongue. It would seem here from a limited number of specimens that more than one species is represented, but allocation of material is not readily evident.

A revision of the Eocene tapiroids undertaken by Leonard Radinsky at Yale University should furnish information having a direct bearing on this problem.

## HYRACHYIDAE

### HYRACHYUS, cf. MODESTUS (Leidy)

(Plate 12, figures 3 and 4)

*Hyrachyus* is now known to be represented in the Cathedral Bluffs member in the three principal areas in which these beds are exposed. In addition to the specimen which includes the M<sup>3</sup> (U.S.N.M. No. 22771; pl. 12, fig. 3) discussed in 1952, there is another associated lot of tooth fragments from the New Fork beds which includes a complete P<sup>4</sup> (U.S.N.M. No. 22772; pl. 12, fig. 4), and an isolated P<sub>4</sub>. The partial dentitions from the Cathedral Bluffs of the Washakie Basin were described and figured by Morris (1954). Not previously recorded is a lower jaw with P<sub>2</sub>-M<sub>3</sub> (U.S.N.M. No. 22773), rather poorly preserved however, from the beds mapped as the Cathedral Bluffs member to the southwest of Continental Peak, near the boundary between Sweetwater and Fremont Counties. All these materials can be closely matched with Bridger specimens that have been referred to one or another of the various species that Wood (1934) has placed in synonymy with *Hyrachyus modestus*, a situation entirely comparable to that noted by Wood for the *Hyrachyus* specimens from the Lost Cabin beds of the Wind River Basin. So far no material that can be referred to this genus has been found in the Knight beds below the Tipton tongue.

## ARTIODACTYLA

### DICHOBUNIDAE

#### DIACODEXIS, cf. METSIACUS (Cope)

Five lower jaw fragments, one of these (U.S.N.M. No. 22240) with P<sub>4</sub>, M<sub>1</sub>, and M<sub>3</sub>, and a second (U.S.N.M. No. 22241) with



M<sub>2</sub>-M<sub>3</sub>, from the Gray Bull horizon of the Knight west of Elk Mountain in the Fossil Basin represent *Diacodexis*, and may well be of the common Wasatchian form of the Bighorn Basin, *Diacodexis metsiacus*. An M<sub>3</sub> in one jaw portion (U.S.N.M. No. 22242) would appear to be large for this species, but it is not as large as that indicated by Sinclair (1914, p. 293) for *Diacodexis robustus*. Reasons for regarding *D. metsiacus* distinct from *D. chacensis* were previously (Gazin, 1952, p. 71) stated.

Isolated teeth from the Gray Bull levels at Bitter Creek Station and in the Red Desert east of Steamboat Mountain may also represent this species, as well as a last lower molar from the Wasatchian of uncertain level just to the north of Tipton Butte.

The two jaws from the type Knight near Knight Station, cited by Van Houten (1945, p. 458; see also Gazin, 1952, p. 72) as *Diacodexis*, sp., have since been located in the American Museum collections and found to be of *Hexacodus*.

#### DIACODEXIS, near D. SECANS (Cope)

A second specimen in the La Barge fauna representing a species of *Diacodexis* that appears to be somewhat larger than *D. metsiacus* was found to the west of Big Piney by N. P. Privrasky of the U. S. Geological Survey near the area mapped as Almy by Schultz (1914). The jaw (U.S.N.M. No. 22243) contains only the last lower molar, which is slightly larger than that in No. 19218 from 12 miles north of Big Piney. An upper molar (U. of C. No. 43885) from near Dad, however, seems relatively small for this species. Possibly this should have been referred to *D. metsiacus*, but, in the absence of information concerning range in size of teeth of *D. secans*, it is tentatively included here because of the horizon represented. An incomplete M<sub>3</sub> in the New Fork collections may also be included with these as possibly representing *Diacodexis secans*.

#### DIACODEXIS, cf. ROBUSTUS Sinclair

Some jaw fragments and teeth, including an upper and two lower molars of a large form of *Diacodexis* were found by McKenna's party near Dad, Wyo. The specimens have the University of California number 46707 but evidently they do not all come from the same individual. The teeth are of a size comparable to those from the Gray Bull described by Sinclair (1914) as *Diacodexis robustus*. The relative width of M<sub>1</sub>, however, might suggest a closer relationship to much smaller *Diacodexis olseni*, which is a Lost Cabin species. A

large  $M_2$ , though, does not appear to be relatively so wide as in *D. olseni*. I suspect that *Diacodexis olseni* may be no more than a variant of *Diacodexis secans*, whereas *D. robustus* would appear to be a distinctive species in Gray Bull time and may have continued on into Lost Cabin time in the Washakie Basin.

**BUNOPHORUS, cf. MACROPTERNUS (Cope)**

(Plate 14, figures 6 and 8)

An additional lower jaw of *Bunophorus*, cf. *macropternus* exhibiting  $P_3$ - $P_4$  and  $M_2$ - $M_3$  (U.S.N.M. No. 22445) was encountered in 1959 in the Knight beds beneath the Fontenelle tongue in the upper part of the Green River Basin. Also, an isolated  $M_3$  (No. 43823) in the University of California collection from beneath the Tipton tongue south of Dad, Wyo., may well represent the same species. The latter is a little smaller than  $M_3$  in No. 19210 (pl. 14, fig. 8) or No. 22445 from near Big Piney tentatively referred to *B. macropternus*, but is less worn. It shows no evidence of a paraconid.

**BUNOPHORUS, cf. ETSAGICUS (Cope)**

(Plate 14, figures 7 and 9)

A lower jaw (U.S.N.M. No. 22244) with  $M_1$ - $M_3$  (pl. 14, fig. 9) and an isolated  $M^3$ , apparently belonging to a species of *Bunophorus*, were found in the New Fork beds to the east and southeast of Big Piney. Teeth in the lower jaw are only a little longer than those in *Bunophorus*, cf. *macropternus*, from beneath the Fontenelle tongue, but are much broader. They appear also to be possibly a little lower cusped and with less evidence of a cingulum, in addition to a somewhat more inflated appearance.

The  $M^3$  (U.S.N.M. No. 22245; pl. 14, fig. 7), if correctly referred, shows that upper teeth of the New Fork species were slightly larger but with lower and more inflated-appearing cusps than the form in the La Barge fauna.

**HEXACODUS PELODES Gazin**

(Plate 7, figure 2; plate 14, figures 1-4)

Several more specimens of *Hexacodus pelodes* have been found in the Knight exposures in the vicinity of Big Piney and La Barge, and lower jaw portions that are referred to this species have also been discovered in the New Fork beds (pl. 14, fig. 4). Moreover, a jaw fragment with a single lower molar in the University of California

collection (No. 43799) shows this form to be represented in the Dad fauna from beneath the Tipton tongue in the Washakie Basin, and two last lower molars from the Cathedral Bluffs tongue above, identified by Morris (1954, p. 197) as *Microsus*, I cannot distinguish from this tooth in *H. pelodes*.

The two jaws from the Knight at Knight Station, earlier referred to *Diacodexis*?, sp. (1952, p. 72), have since been located in the American Museum collections and found to represent *Hexacodus*. One of them, A.M. No. 12843, may well be of *H. pelodes*, to judge by the preserved molar, although  $P_4$  is relatively slender and lacks both paraconoid and metaconid, suggesting a distinct species. However, this tooth seems highly variable in *H. pelodes*, between specimens in which the molars cannot be distinguished. In fact, no two  $P_4$ 's among these have been found that are quite alike.

Of particular interest is the discovery, in recent collections representing the La Barge fauna, of upper teeth that may belong to this small artiodactyl. One specimen is a maxillary fragment with  $M^1$  and  $M^2$  (U.S.N.M. No. 22248; pl. 14, fig. 1) and another an isolated upper molar (U.S.N.M. No. 22434; pl. 14, fig. 3), possibly  $M^1$ . A second maxilla regarded as belonging to *Hexacodus pelodes*, found by a University of Wyoming field party (U. of Wyo. No. 1779) in the La Barge horizon, is important in displaying  $P^3$  and  $P^4$  as well as  $M^2$  and part of  $M^1$  (pl. 7, fig. 2). The premolars are comparatively large, as would be expected from consideration of the large and somewhat inflated lower fourth premolar, and exhibit an enamel rugosity more evident than in the molars. The talon, moreover, is broad and prominent in both  $P^3$  and  $P^4$  and has a well-developed deutercone. No tritocone is present.

Among other Wasatchian artiodactyls,  $P^3$  is known in both *Diacodexis* and *Wasatchia*. In *Diacodexis* this tooth is much more elongate, anteroposteriorly, and the talon is not nearly so well developed. It exhibits, moreover, a more prominent parastyle and a distinctive tritocone, quite unlike *Hexacodus*. Sinclair's illustration of  $P^3$  (1914, fig. 2) in *Wasatchia dorsejana* shows this tooth to be relatively small and with little evidence of a talon.  $P^4$  in No. 1779 is rather less distinctive but in comparison with *Diacodexis* it is seen to have more inflated cusps with a higher saddle between them.

Among Bridgerian artiodactyls,  $P^3$  is recorded only for *Homacodon*. This tooth in *Hexacodus* is more suggestive of *Homacodon* than it is of *Diacodexis*, but the anteroposteriorly broader talon and the absence of a tritocone distinguish it from *Homacodon*.  $P^4$ , again, is rather less



distinctive and resembles that in *Helohyus* and *Antiacodon* as well as *Homacodon*. A difference, however, perhaps more noticeable with reference to *Antiacodon* and *Homacodon* than to *Helohyus*, lies in the higher, more inflated appearance of the deuterocone and somewhat less transverse width of the tooth.

The upper molars, as exhibited in U.S.N.M. No. 22248 and U. of Wyo. No. 1779, have a rectangular appearance, rather distinctive in comparison with *Diacodexis*. The protocone, though well developed, is not so large and inflated as in *Diacodexis* and the accessory cusps, the protoconule and metaconule, are larger and more conical than in that genus. Particularly noticeable is the strong development of the cingulum anterointernally and posterointernally, and weakly or not at all across the protocone, giving the talon a square appearance. Anterointernally, the nearly right-angle flexure of the cingulum shows little or no evidence of a cuspule. Posterointernally, the cingulum rises distinctly to form a low, well-separated hypocone with a slight crest extending away from the cingulum toward the metaconule on  $M^1$ , but toward the protocone on  $M^2$ .

The upper molars, believed to be of *Hexacodus pelodes*, are seen to resemble much more closely those of *Microsus* and *Homacodon* than they do those of contemporary *Diacodexis*; although the hypocone is much less developed and the accessory cusps have better-defined crests than in the Bridger genera. *Homacodon* differs from *Microsus* essentially in more inflated cusps and shows development of the cingulum lingually in upper molars. In the cf. *Hexacodus* specimens the crest from the anterior portion of the metaconule to the anterointernal part of the metacone and the posterior crest from the metaconule to the cingulum are more pronounced. In A.M. No. 12146 of *Microsus cuspidatus* this posterior crest is absent, but in A.M. No. 12696 it is weakly developed. A.M. No. 12696 of *M. cuspidatus* resembles cf. *H. pelodes* in almost every way except in greater development and more conical form of hypocone and generally more subdued crests. It should be noted, moreover, that while the hypocone of cf. *H. pelodes* rises from the cingulum, in certain specimens of *Microsus*, though not all, the cingulum has become developed part way around the hypocone. Furthermore, the anterointernal angle of  $M_2$  in cf. *H. pelodes* is a little less rounded than in *Microsus* and both molars show a slight mesostyle or rise in the cingulum more suggestive of *Antiacodon*.

In *Antiacodon*, as represented by A.M. No. 12043, the cusps of the upper molars are very conical and the hypocone in  $M_3$ , at the lingual



extremity of the posterior cingulum, is about the size of the protoconule and metaconule, larger than in cf. *Hexacodus pelodes* but smaller than in *Microsus*. The protocone in *Antiacodon* is relatively larger and does not appear so forward as in either of these. The relative position of the protocone apparently results from the development of an anterointernal cusp at the lingual extremity of the anterior cingulum, immediately anterior to the protocone. It is smaller than the accessory cusps, but rather distinctive.

It would seem from the foregoing that although the lower jaws of *Hexacodus pelodes* most strongly suggest *Antiacodon* among the latter forms, with some variation in the direction of *Microsus*, Knight upper molars thought to be of *Hexacodus* are somewhat more suggestive of *Microsus*, that is, if upper teeth of *Antiacodon* (A.M. No. 12043) are properly referred. Possibly a second genus is represented by the Knight upper teeth, but I am more inclined to believe that variation within the genus, as noted, for example, in the varied development of  $P_4$  in *H. pelodes*, may be sufficient to accommodate ancestry for more than one of the bunodont artiodactyls of the Bridger. With regard to this it may be noted that, although premolars are not known, the lower molars of *H. uintensis*, with their somewhat longer trigonids than in *H. pelodes*, could possibly have given rise to those of *Helohyus*. Bridger *Helohyus*, in addition to greater size, differs from the earlier form, so far as known, only in more inflated cusps with some reduction of the posterior cingulum and its hypoconulid.

MEASUREMENTS IN MILLIMETERS OF UPPER TEETH  
IN CF. *Hexacodus pelodes*

	U.S.N.M. No. 22248	U. of Wyo. No. 1779
$P^3$ , anteroposterior diameter: greatest transverse diameter .....		4.3:4.3
$P^4$ , anteroposterior diameter: greatest transverse diameter .....		4.1:5.1
$M^1$ , anteroposterior diameter buccally: transverse diameter of anterior portion.....	4.2:4.8	
$M^2$ , anteroposterior diameter buccally: transverse diameter of anterior portion.....	4.6:5.8	4.7:5.6

HEXACODUS UINTENSIS Gazin

(Plate 14, figure 5)

A second jaw portion of *Hexacodus uintensis* has been found in the vicinity of Fossil Butte in the Fossil Basin. The preserved  $M_2$  (U.S.N.M. No. 22250) corresponds almost exactly to that in the type

(P.U. No. 16175) and was found at about the same level in the Knight but in the patch of Badlands forming the saddle to the north of Fossil Butte. Also the second of the two jaws from Knight Station, earlier referred to as *Diacodexis*? sp. (1952, p. 72), since located in the American Museum collections and found to be of *Hexacodus*, evidently represents the larger *H. uintensis*. The specimen (A.M. No. 12844) includes  $M_2$  and  $M_3$  and is seen to correspond closely in the form of  $M_2$  to the type. The other specimen, A.M. No. 12843, from Knight Station, as discussed in the preceding section, appears to be of *Hexacodus pelodes*.

A careful search of Gray Bull materials from the Bighorn Basin in both the American Museum and National Museum collections has turned up only one specimen of *Hexacodus* among materials labeled *Diacodexis*. The specimen (A.M. No. 4140) is a lower jaw with  $M_2$  and  $M_3$  and resembles most closely *Hexacodus uintensis* in the relative proportions of the lower molar trigonids. It is interesting to note that this was the specimen selected by Osborn to typify *Trigonolestes* (= *Diacodexis*) *metisiacus* in his "Evolution of Mammalian Molar Teeth" (1907, p. 171, fig. 152B). *Hexacodus* is evidently very rare in the Gray Bull horizon and so far has not been observed in this level of the Knight. It has not been found, or at least not recognized, in any of the horizons of the Wind River Basin, or the higher levels of the Bighorn Wasatchian.

#### REFERENCES

BRADLEY, WILMOT H.

1959. Revision of stratigraphic nomenclature of Green River formation of Wyoming. Bull. Amer. Assoc. Petrol. Geol., vol. 43, No. 5, pp. 1072-1075.

COPE, EDWARD D.

1872. On the dentition of *Metalophodon*. Proc. Amer. Philos. Soc., vol. 12, pp. 542-545.
1873. On the new perissodactyles from the Bridger Eocene. Proc. Amer. Philos. Soc., vol. 13, pp. 35-36.
1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Rep. U. S. Geogr. Surv. West of 100th Meridian (Wheeler), vol. 4, pt. 2, pp. i-iv, 1-370, pls. 22-83.
1884. The Vertebrata of the Tertiary formations of the West. Book 1. Rep. U. S. Geol. Surv. Terr. (Hayden), vol. 3, pp. i-xxxiv, 1-1009, figs. 1-38, pls. 1-75a.

DENISON, ROBERT H.

1938. The broad-skulled pseudocreodi. Ann. New York Acad. Sci., vol. 37, art. 3, pp. 163-256, figs. 1-32.

## DONOVAN, J. H.

1950. Intertonguing of Green River and Wasatch formations in part of Sublette and Lincoln Counties, Wyoming. Wyoming Geol. Assoc., 5th Ann. Field Conf., Southwest Wyoming Guidebook, pp. 59-67, 2 pls.

## DORR, JOHN A., JR.

1958. *Prouintatherium*, new uinathere genus, earliest Eocene, Hoback formation, Wyoming, and the phylogeny of Dinocerata. Journ. Paleont., vol. 32, No. 3, pp. 506-516.

## EARLE, CHARLES.

1892. Revision of the species of *Coryphodon*. Bull. Amer. Mus. Nat. Hist., vol. 4, No. 1, pp. 149-166, figs. 1-2, 1 table, pls. 75-77.

## GAZIN, C. LEWIS.

1936. A taeniodont skull from the lower Eocene of Wyoming. Proc. Amer. Philos. Soc., vol. 76, No. 5, pp. 597-612, figs. 1-2, pls. 1-5.
1952. The lower Eocene Knight formation of western Wyoming and its mammalian faunas. Smithsonian Misc. Coll., vol. 117, No. 18, pp. 1-82, figs. 1-6, pls. 1-11.
1953. The Tillodontia: an early Tertiary order of mammals. Smithsonian Misc. Coll., vol. 121, No. 10, pp. 1-110, figs. 1-38, pls. 1-16.
- 1956a. The occurrence of Paleocene mammalian remains in the Fossil Basin of southwestern Wyoming. Journ. Paleont., vol. 30, No. 3, pp. 707-711, 1 fig.
- 1956b. The upper Paleocene Mammalia from the Almy formation in western Wyoming. Smithsonian Misc. Coll., vol. 131, No. 7, pp. 1-18, pls. 1-2.
1958. A review of the middle and upper Eocene primates of North America. Smithsonian Misc. Coll., vol. 136, No. 1, pp. 1-112, 1 chart, pls. 1-14.
1959. Paleontological exploration and dating of the early Tertiary deposits in basins adjacent to the Uinta Mountains. Intermountain Assoc. Petrol. Geol., 10th Ann. Field Conf. Guidebook, pp. 131-138, 1 fig.
1961. New sciuravid rodents from the lower Eocene Knight formation of western Wyoming. Proc. Biol. Soc., Washington, vol. 74, art. 21, pp. 193-194.

## GRANGER, WALTER.

1914. On the names of lower Eocene faunal horizons of Wyoming and New Mexico. Bull. Amer. Mus. Nat. Hist., vol. 33, art. 15, pp. 201-207.
1915. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 3—Order Condylarthra. Families Phenacodontidae and Meniscotheriidae. Bull. Amer. Mus. Nat. Hist., vol. 34, art. 10, pp. 329-361, figs. 1-18.

## HAYDEN, FERDINAND V.

1869. Preliminary report (3d ann.) of the U. S. Geological Survey of Colorado and New Mexico, pp. 91-92.

## JEPSEN, GLENN L.

1930. New vertebrates from the lower Eocene of the Bighorn Basin, Wyoming. Proc. Amer. Philos. Soc., vol. 69, No. 4, pp. 117-131, pls. 1-4.

1934. A revision of the American Apatemyidae and the description of a new genus, *Sinclairiella*, from the White River Oligocene of South Dakota. Proc. Amer. Philos. Soc., vol. 74, No. 4, pp. 287-305, figs. 1-4, pls. 1-3.
- KELLEY, DANA R., and WOOD, ALBERT E.  
1954. The Eocene mammals from the Lysite member, Wind River formation of Wyoming. Journ. Paleont., vol. 28, No. 3, pp. 337-366, figs. 1-15.
- KITTS, DAVID B.  
1956. American *Hyracotherium* (Perissodactyla, Equidae). Bull. Amer. Mus. Nat. Hist., vol. 110, art. 1, pp. 1-60, figs. 1-10, pls. 1-7.
- LOOMIS, FREDERIC B.  
1905. The Hyopsodidae of the Wasatch and Wind River Basins. Amer. Journ. Sci., vol. 19, pp. 416-424, figs. 1-8.  
1906. Wasatch and Wind River primates. Amer. Journ. Sci., vol. 21, pp. 277-285, figs. 1-8.  
1907. Wasatch and Wind River rodents. Amer. Journ. Sci., vol. 23, pp. 123-130, figs. 1-7.
- MARSH, OTHNIEL C.  
1876. Notice of new Tertiary mammals. V. Amer. Journ. Sci., vol. 12, pp. 401-404.
- MATTHEW, WILLIAM D.  
1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Mem. Amer. Mus. Nat. Hist., vol. 9, pt. 6, pp. 291-567, figs. 1-118, pls. 42-52.  
1915a. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 1.—Order Ferae (Carnivora). Suborder Creodonta. Bull. Amer. Mus. Nat. Hist., vol. 34, art. 1, pp. 1-103, figs. 1-87.  
1915b. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 2.—Order Condylarthra, family Hyopsodontidae. Bull. Amer. Mus. Nat. Hist., vol. 34, art. 9, pp. 311-328, figs. 1-10.  
1915c. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 4.—Entelonychia, Primates, Insectivora (part). Bull. Amer. Mus. Nat. Hist., vol. 34, art. 14, pp. 429-483, figs. 1-52, pl. 15.  
1918. A revision of the lower Eocene Wasatch and Wind River faunas. Pt. 5.—Insectivora (cont.), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 565-657, figs. 1-68.
- MCGREW, PAUL O., and ROEHLER, HENRY W.  
1960. Correlation of Tertiary units in southwestern Wyoming. Wyoming Geol. Assoc., 15th Ann. Field Conf. Guidebook, pp. 156-158, 1 chart.
- McKENNA, MALCOLM C.  
1960. Fossil Mammalia from early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. California Publ. Geol. Sci., vol. 37, No. 1, pp. 1-130, figs. 1-64.
- MORRIS, WILLIAM J.  
1954. An Eocene fauna from the Cathedral Bluffs tongue of the Washakie Basin, Wyoming. Journ. Paleont., vol. 28, No. 2, pp. 195-203, 1 fig., pls. 21-22.



## NACE, RAYMOND L.

1939. Geology of the northwest part of the Red Desert, Sweetwater and Fremont Counties, Wyoming. Geol. Surv. Wyoming Bull. 27, pp. 1-51, 6 figs., 3 pls.

## NIGHTINGALE, WILLIAM T.

1930. Geology of Vermilion Creek gas area in southwest Wyoming and northwest Colorado. Bull. Amer. Assoc. Petrol. Geol., vol. 14, No. 8, pp. 1013-1040, figs. 1-5, 2 tables.

## OSBORN, HENRY F.

1898. Evolution of the Amblypoda. Part 1. Taligrada and Pantodonta. Bull. Amer. Mus. Nat. Hist., vol. 10, art. 11, pp. 169-218, figs. 1-29.  
1907. Evolution of mammalian molar teeth. Pp. i-ix, 1-250, figs. 1-215. New York.

## PIPIRINGOS, GEORGE N.

1955. Tertiary rocks in the central part of the Great Divide Basin, Sweetwater County, Wyoming. Wyoming Geol. Assoc., Guidebook 10th Ann. Field Conf., pp. 100-104.

## SCHULTZ, ALFRED R.

1914. Geology and geography of a portion of Lincoln County, Wyoming. U. S. Geol. Surv. Bull. 543, pp. 1-141, figs. 1-8, pls. 1-11.

## SIMPSON, GEORGE G.

1931. *Metacheiromys* and the Edentata. Bull. Amer. Mus. Nat. Hist., vol. 59, pp. 295-381, figs. 1-23.  
1937. Notes on the Clark Fork, upper Paleocene, fauna. Amer. Mus. Novitates, No. 954, pp. 1-24, figs. 1-6.  
1940. Studies on the earliest primates. Bull. Amer. Mus. Nat. Hist., vol. 77, art. 4, pp. 185-212, figs. 1-8.  
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i-xvi, 1-350.  
1948. The Eocene of the San Juan Basin, New Mexico. Amer. Journ. Sci., vol. 246, pp. 257-282, 363-385.  
1954. An apatemyid from the early Eocene of New Mexico. Amer. Mus. Novitates, No. 1654, pp. 1-4, 1 fig.  
1955. The Phenacolemuridae, new family of early primates. Bull. Amer. Mus. Nat. Hist., vol. 105, art. 5, pp. 415-441, tables 1-6, pls. 30-35.

## SINCLAIR, WILLIAM J.

1914. A revision of the bunodont Artiodactyla of the middle and lower Eocene of North America. Bull. Amer. Mus. Nat. Hist., vol. 33, art. 21, pp. 267-295, figs. 1-28.

## THORPE, MALCOLM R.

1934. *Meniscotherium robustum* sp. nov. and a discussion of *Hyracops socialis* Marsh. Amer. Journ. Sci., vol. 27, pp. 401-409, figs. 1-6.

## TRACEY, JOSHUA I., JR., and ORIEL, STEPHEN S.

1959. Uppermost Cretaceous and lower Tertiary rocks of the Fossil Basin. Intermountain Assoc. Petrol. Geol., 10th Ann. Field Conf. Guidebook, pp. 126-130, 1 fig., 1 table.

## VAN HOUTEN, FRANKLYN B.

1945. Review of latest Paleocene and early Eocene mammalian faunas. Journ. Paleont., vol. 19, No. 5, pp. 421-461.

## VEATCH, ARTHUR C.

1907. Geography and geology of a portion of southwestern Wyoming. U. S. Geol. Surv. Prof. Pap. No. 56, pp. i-iv, 1-178, figs. 1-9, pls. 1-26.

## WHITE, THEODORE E.

1952. Preliminary analysis of the vertebrate fossil fauna of the Boysen Reservoir area. Proc. U. S. Nat. Mus., vol. 102, pp. 185-207, figs. 75-79, 1 map.

## WILLIAMS, NORMAN C., and MADSEN, JAMES H., JR.

1959. Late Cretaceous stratigraphy of the Coalville area, Utah. Inter-mountain Assoc. Petrol. Geol., 10th Ann. Field Conf. Guidebook, pp. 122-125, figs. 1-3.

## WILSON, ROBERT W.

1938. Review of some rodent genera from the Bridger Eocene. Pts. I-III. Amer. Journ. Sci., vol. 35, pp. 123-137, 207-222, 297-304, figs. 1-15.

## WOOD, HORACE E., II.

1934. Revision of the Hyrachyidae. Bull. Amer. Mus. Nat. Hist., vol. 67, art. 5, pp. 181-295, figs. 1-15, pls. 20-24.

## WOOD, HORACE E., II, ET AL.

1941. Nomenclature and correlation of the North American Continental Tertiary. Bull. Geol. Soc. Amer., vol. 52, pp. 1-48, pl. 1.

## WORTMAN, JACOB L.

1896. Species of *Hyracotherium* and allied perissodactyls from the Wahsatch and Wind River beds of North America. Bull. Amer. Mus. Nat. Hist., vol. 8, art. 6, pp. 81-110, 3 tables, figs. 1-18, 1 pl.  
1897. The Ganodonts and their relationship to the Edentata. Bull. Amer. Mus. Nat. Hist., vol. 9, art. 6, pp. 59-110, figs. 1-36.

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## PLATE 13

HYRACOTHERIUM AND HEPTODON FROM THE LOWER EOCENE  
OF WYOMING

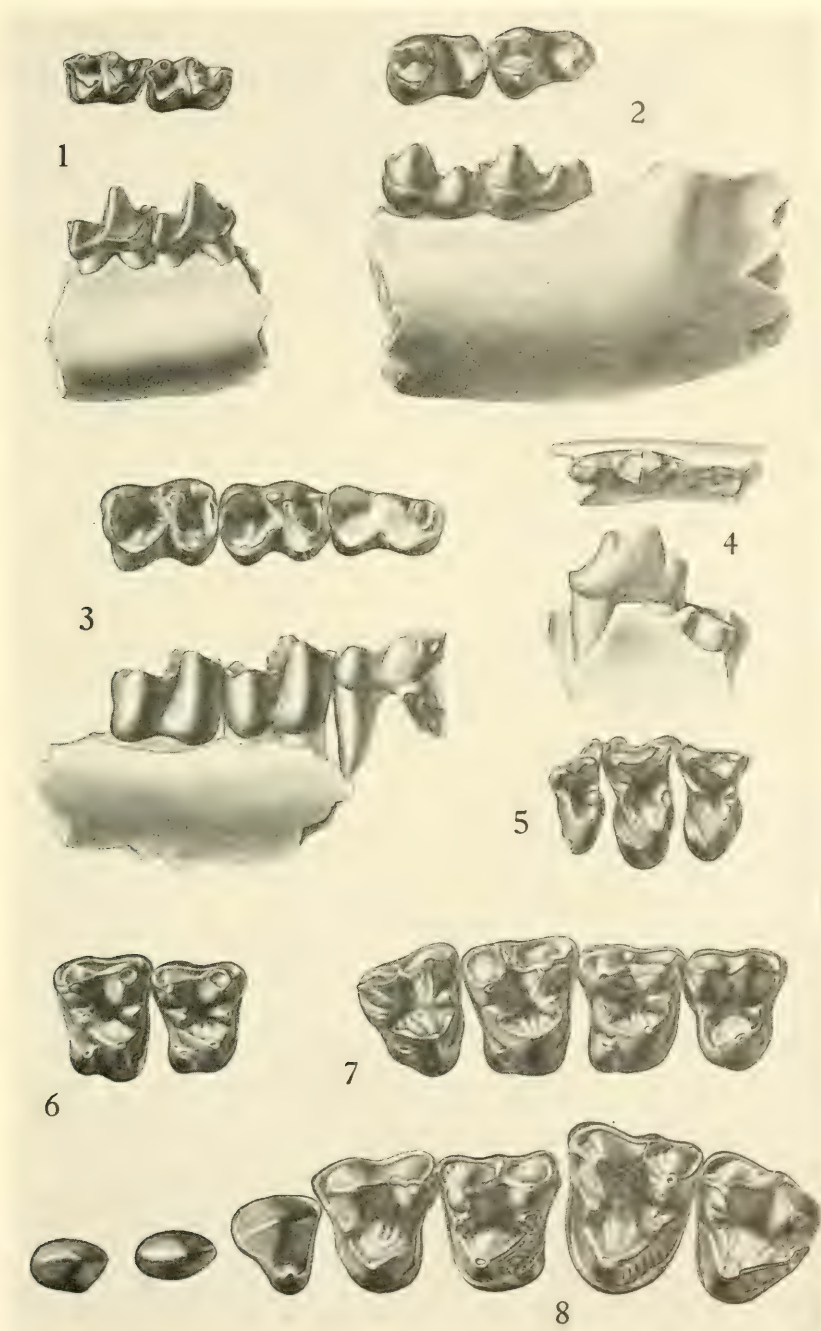
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7, Left upper premolars, P <sup>3</sup> -P <sup>4</sup> (U.S.N.M. No. 19744), occlusal view. 2 × natural size. La Barge, Green River Basin, Wyoming.	
8, Left upper premolars, P <sup>2</sup> -P <sup>4</sup> (U.S.N.M. No. 22494), occlusal view. 2 × natural size. La Barge, Green River Basin, Wyoming.	
9, Left upper premolars, P <sup>2</sup> -P <sup>4</sup> (U.S.N.M. No. 22495), occlusal view. 2 × natural size. La Barge, Green River Basin, Wyoming.	
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## PLATE 14

HEXACODUS AND BUNOPHORUS FROM THE LOWER EOCENE OF  
WYOMING

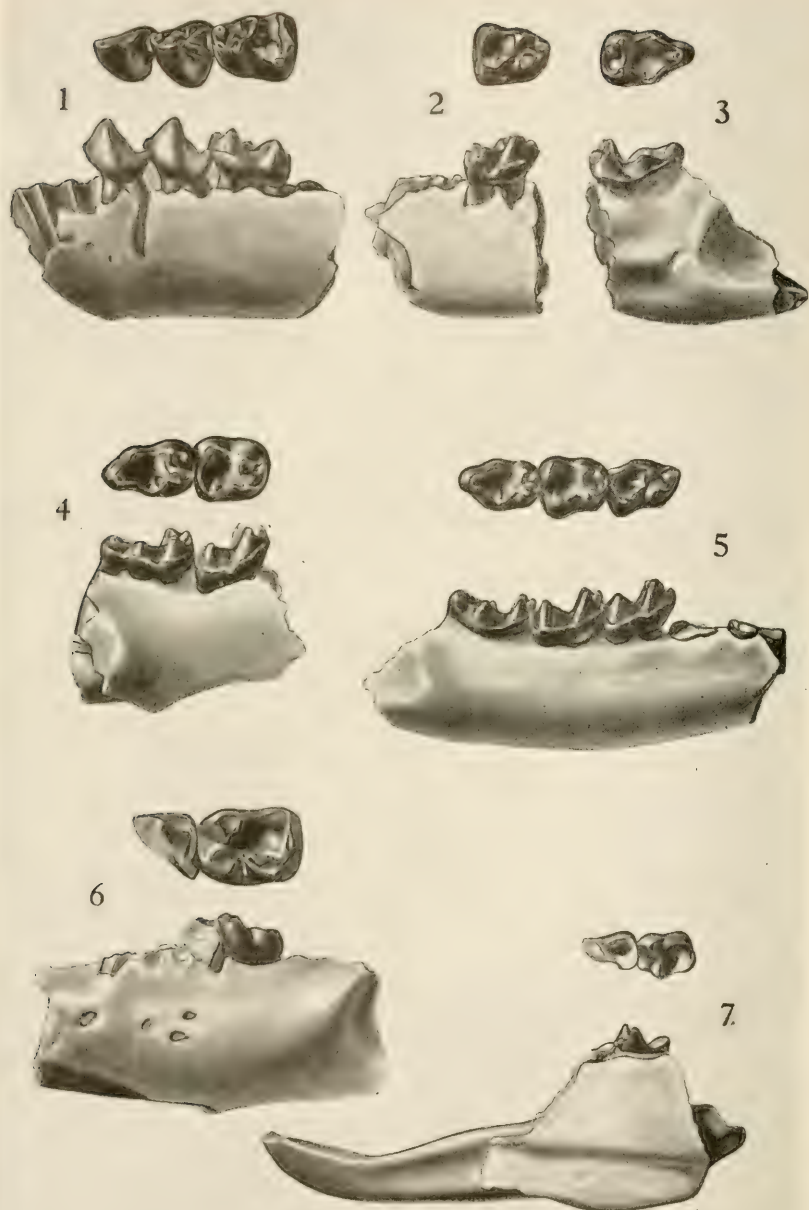
FIGS. 1, 3. Cf. <i>Hexacodus pelodes</i> Gazin.....	82
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MARSUPIAL, INSECTIVORES, PRIMATES, AND TILLODONT FROM  
THE LOWER EOCENE OF WYOMING

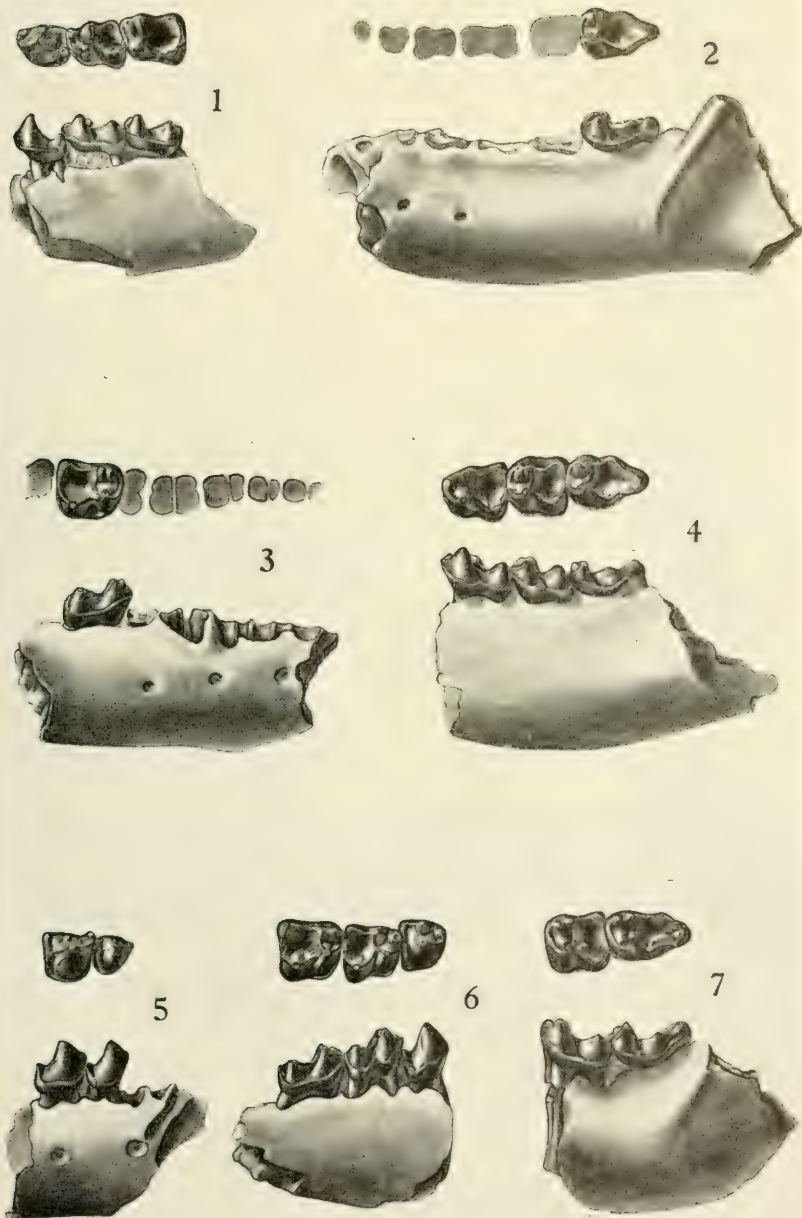
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PRIMATES AND INSECTIVORE FROM THE  
LOWER EOCENE OF WYOMING

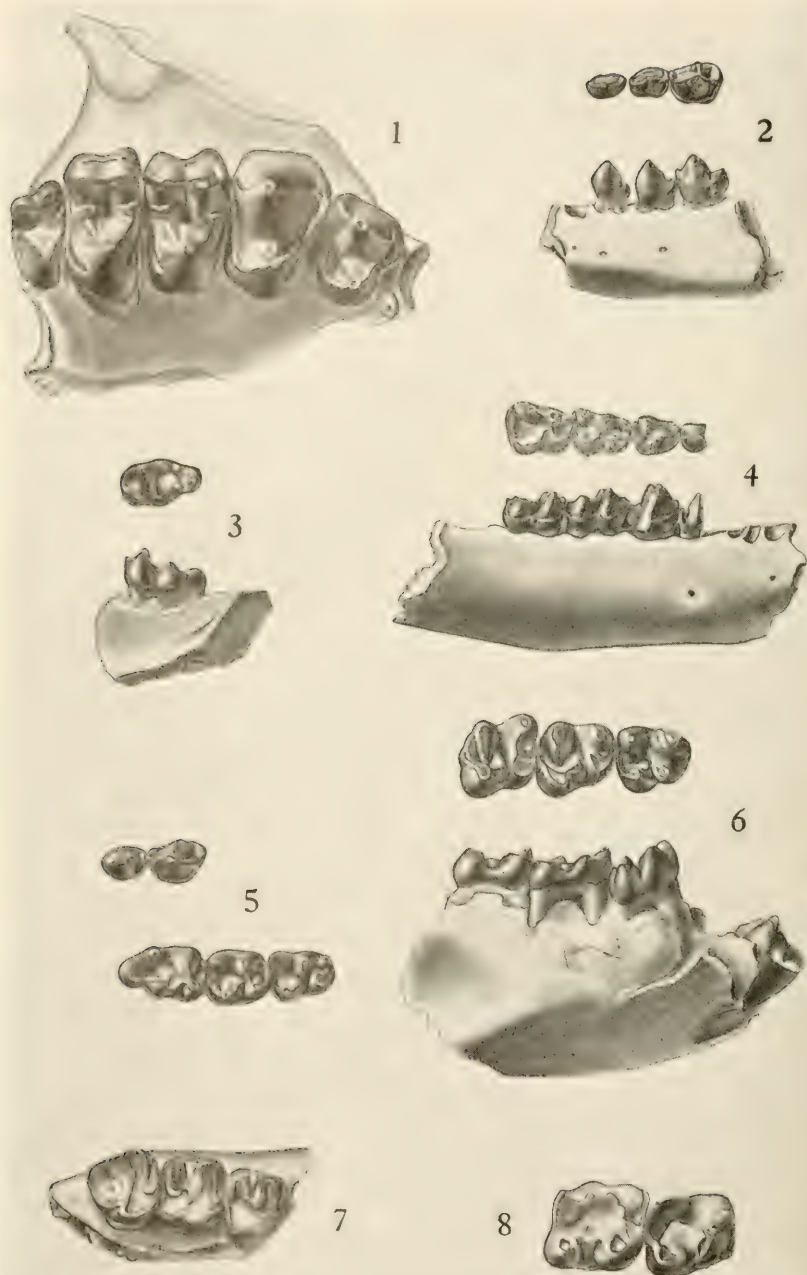
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PRIMATES FROM THE LOWER EOCENE OF WYOMING

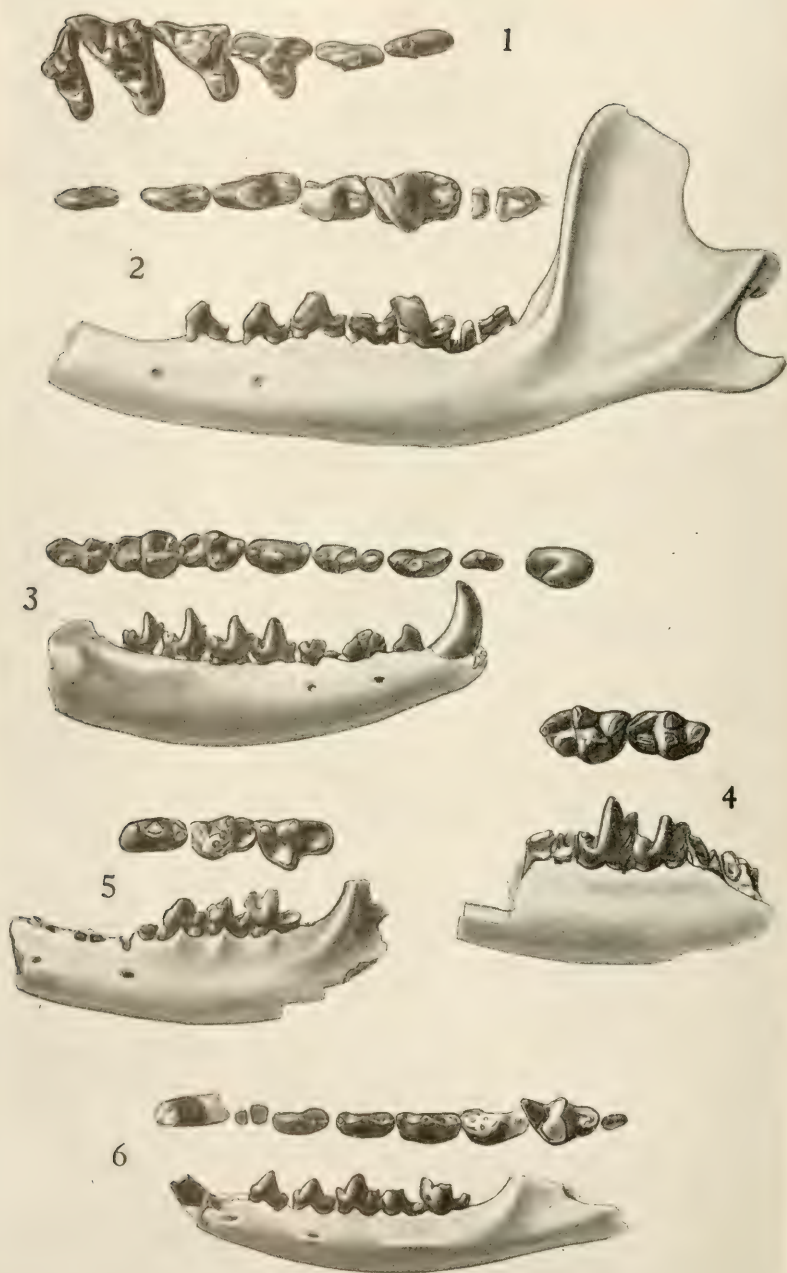
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PRIMATES AND RODENTS FROM THE LOWER EOCENE OF WYOMING  
(SEE EXPLANATION OF PLATES AT END OF TEXT.)



PRIMATES AND RODENTS FROM THE LOWER EOCENE OF WYOMING  
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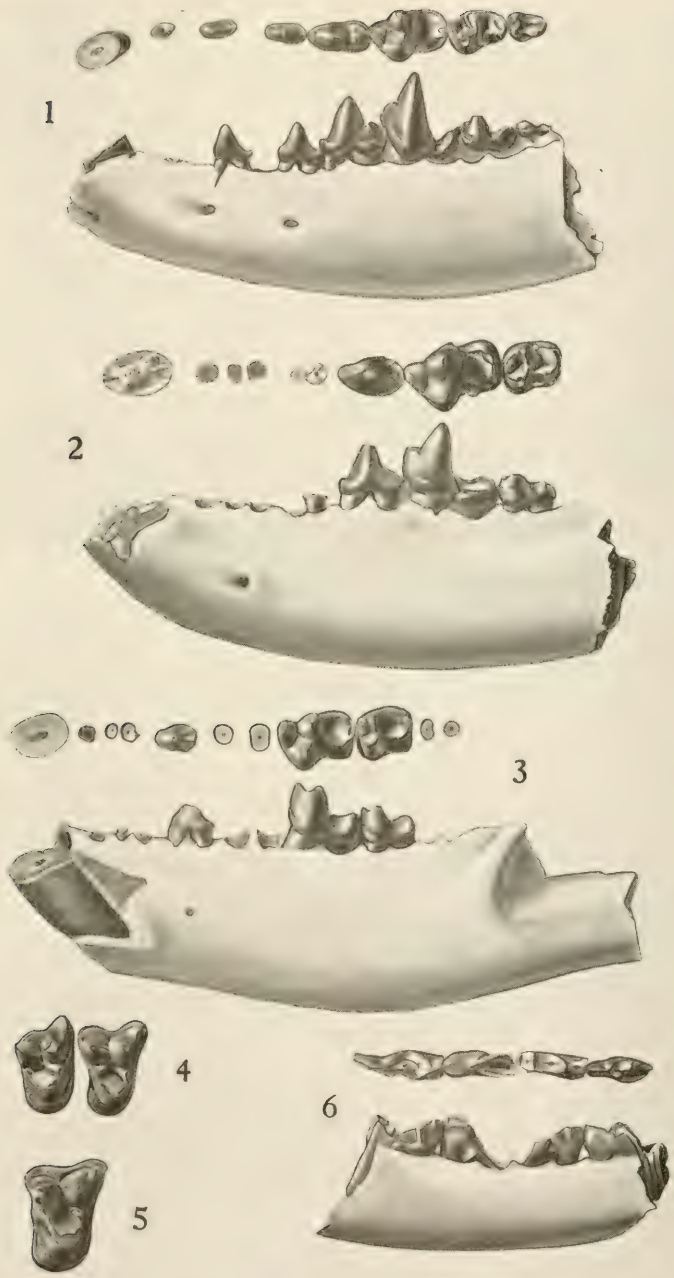
CARNIVORES FROM THE LOWER EOCENE OF WYOMING

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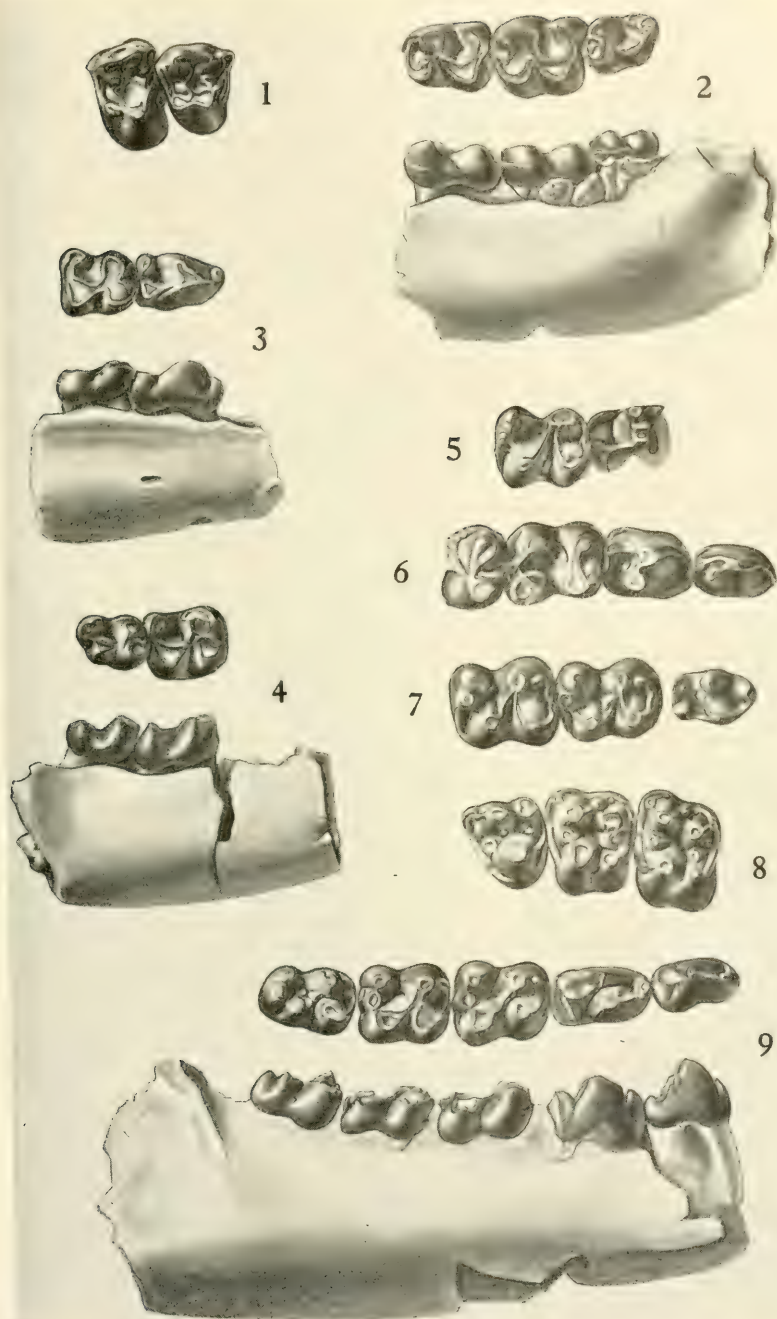




CARNIVORES AND ARTIODACTYL FROM THE  
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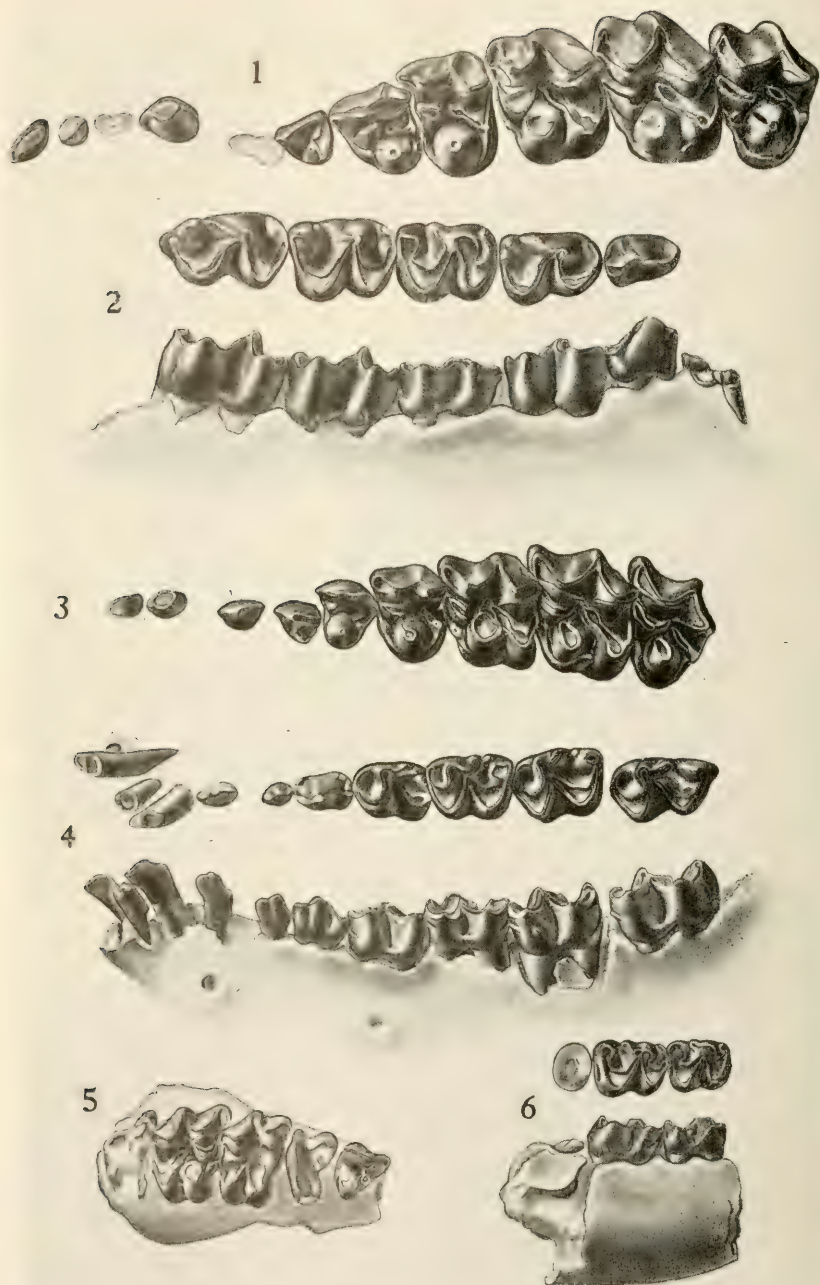


CARNIVORES FROM THE LOWER EOCENE OF WYOMING  
(SEE EXPLANATION OF PLATES AT END OF TEXT.)



CONDYLARTHS FROM THE LOWER EOCENE OF WYOMING

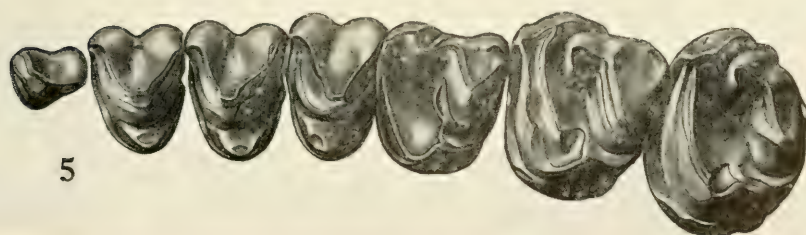
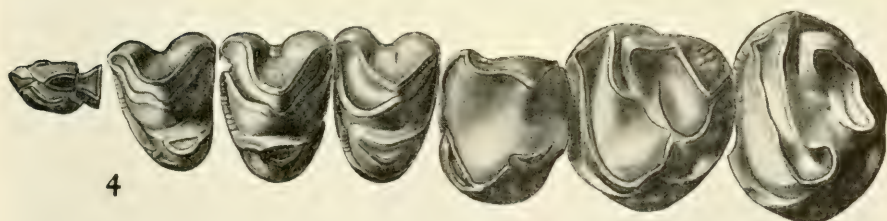
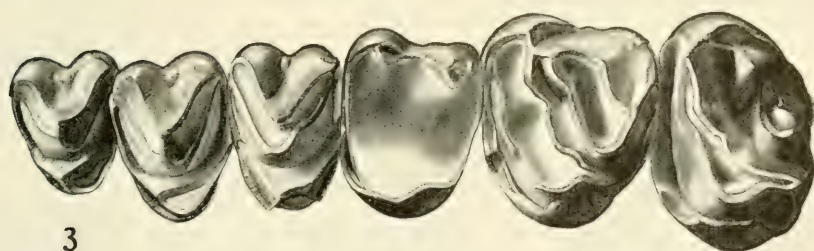
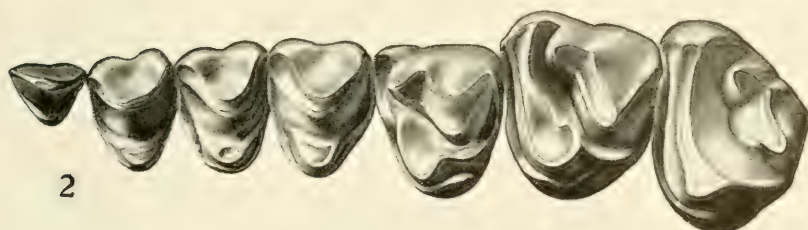
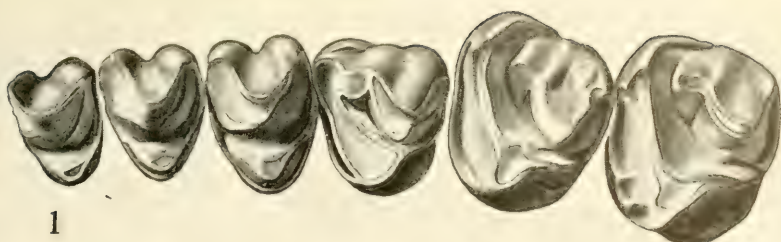
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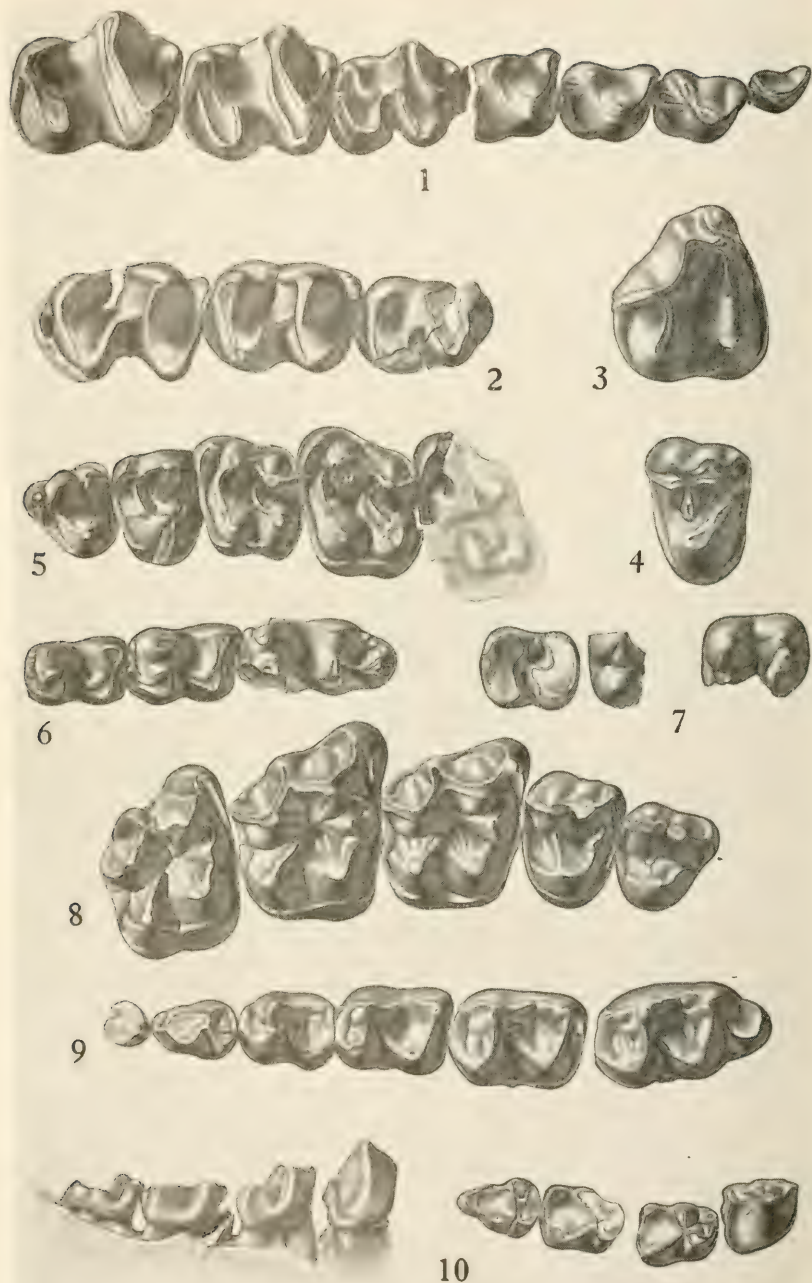
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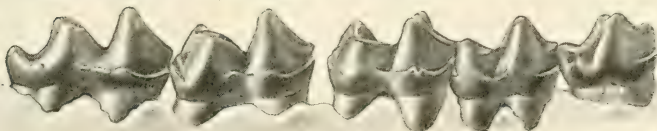
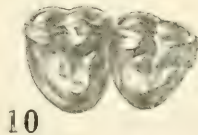
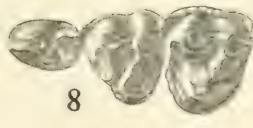
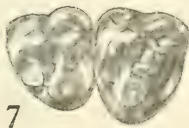
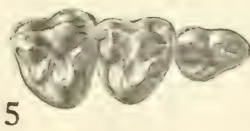
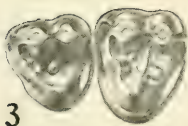
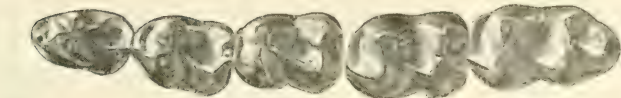
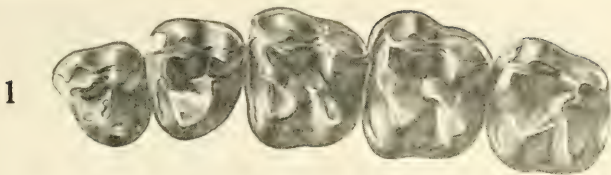
CORYPHODON FROM THE LOWER EOCENE OF WYOMING

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CORYPHODON, PERISSODACTYLS, TAENIODONT, AND PRIMATE FROM  
THE LOWER EOCENE OF WYOMING

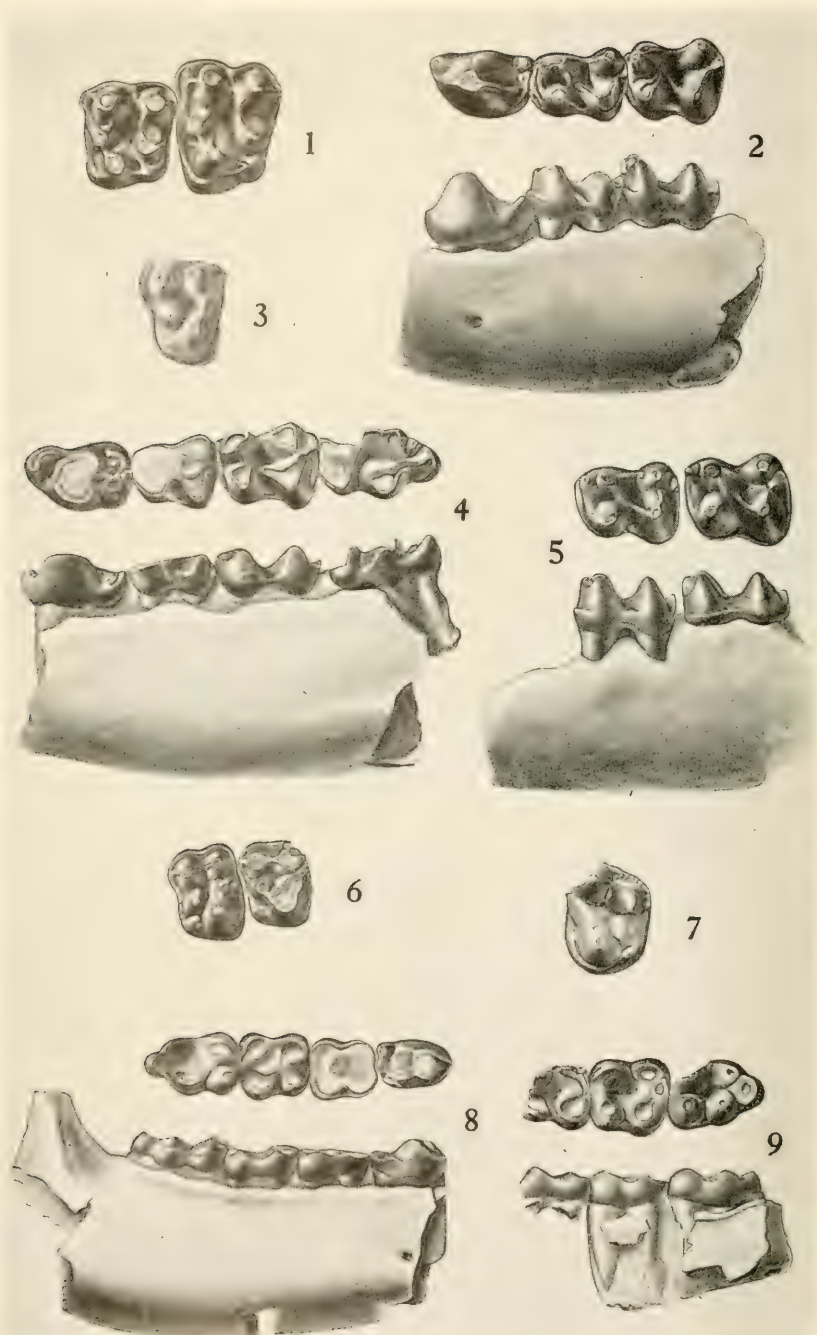
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HYRACOTHERIUM AND HEPTODON FROM THE  
LOWER EOCENE OF WYOMING

(SEE EXPLANATION OF PLATES AT END OF TEXT.)





HEXACODUS AND BUNOPHORUS FROM THE  
LOWER EOCENE OF WYOMING

(SEE EXPLANATION OF PLATES AT END OF TEXT.)







SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 144, NUMBER 2

DIMENSIONAL RELATIONSHIPS  
FOR FLYING ANIMALS

By  
CRAWFORD H. GREENEWALT  
President, E. I. du Pont de Nemours & Co.



(PUBLICATION 4477)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION

April 6, 1962





## FOREWORD

Many of the data on the dimensions of flying animals are found in journals which are not readily accessible. Aside from Sotavalta's papers on insects, published within the past 15 years, the significant references are also many years old, harking back to an era when such studies were undertaken primarily to provide inspiration for the development of aircraft.

The literature is quite extensive for insects, for birds, and even for bats. Furthermore the results of the several investigations appear consistent among themselves, leading to the presumption that a reasonable degree of precision obtains for all the great mass of available data.

It seemed worthwhile first to bring these scattered sources together in one publication, and second to plot the various dimensions against each other to determine how well the principles of dimensional similarity hold for so diverse a collection of flying animals. The figures speak for themselves. The text has been added by way of summary and to point out certain anomalies which appear to provide exceptions to nature's usual sense of orderliness. The scientific names in the tables are given as they appeared in the original publications, in the belief that few identification difficulties will arise.

There is no claim to originality in what follows. I shall be quite content if it is useful, perhaps even stimulating, to entomologists and ornithologists.

CRAWFORD H. GREENEWALT

*Greenville, Delaware*  
*November 1960*



# DIMENSIONAL RELATIONSHIPS FOR FLYING ANIMALS

BY CRAWFORD H. GREENEWALT  
*President, E. I. du Pont de Nemours & Co.*

For a dimensionally similar series of objects, animate or inanimate, a volume or a mass will be proportional to the cube, a surface to the square, of a linear dimension. If Alice, then, after sipping from the bottle labeled "Drink me," were reduced to one-third of her normal height, her surface would be one-ninth, her weight one twenty-seventh, of its original value. Or if we should plot Alice's weight and that of many other little girls, large and small, against let us say the length of their arms, we should find in logarithmic coordinates a straight line whose slope is 3, or in mathematical terms

$$W = cl^3$$

where  $W$  is weight,  $l$  is length of arm, and  $c$  a constant of proportionality.

For cats or for mice the result should be the same with, however, a different value for  $c$ , meaning simply that cats or mice are dimensionally similar within their families but not with each other, or for that matter with little girls.

## BODY WEIGHT AND WING LENGTH

We turn now to figure 1 (all figures follow page 7), on which is plotted total weight against wing length for the entire array of flying animals. We see that for body weights ranging from less than 1 to more than 10 million milligrams, weight is roughly proportional to the cube of the wing length.

Insects show a much greater "scatter" than birds, evidence I suppose of nature's versatility in designing many models of animate aircraft at the lower end of the scale. The highest values of wing length per unit weight are found for the dragonflies and damselflies, for certain butterflies, and for such insect specialties as the crane flies and mosquitoes. Except for the dragonflies, these are rather poor fliers with low wing-beat rates. Lowest relative wing lengths are for the

bumble bees whose bulky, heavy bodies make one wonder how they can manage ever to become airborne. What might be called the "main sequence" of insects falls on a straight line well below that for the birds. One might expect this to mean a generally poorer flight performance, but this does not necessarily follow, since in appraising aerial ability one must also take wing-beat rate and muscle weight into account.

For birds, excluding for the moment the hummingbirds, the scatter is much less, particularly at the small end of the scale. In general the soaring birds have long wings, the gallinaceous birds short wings per unit of total weight. When one considers the aerodynamics of soaring this result might well have been expected.

Hummingbirds fall into a very special group, for here nature appears to have devised an unusual model, one in which weight is proportional to the 1.5 power of the wing length. This result is so unexpected that one might well question its validity. In figure 2 the hummingbird region is expanded, and I have plotted separately the two sets of available data. Their self-consistency leaves little room for doubt of the basic relationship. Hummingbirds cover only a small part of the roster of flying animals, and it should be noted that extrapolation of the hummingbird line either to larger or smaller body weights would lead to aerodynamic monstrosities. I can offer no rationale for the anomaly. Hummingbirds are excellent fliers, and it may be that their peculiar dimensional relationships contribute to this end.

One also sees that the hummingbirds are placed almost exactly in the center of the figure; hence they may represent a zone of transition between insects and other birds.

#### BODY WEIGHT AND WING AREA

Figure 3 shows the relationship between body weight and wing area. The results do not differ significantly from those in figures 1 and 2. Note again the much greater scatter for insects, the increasing scatter for birds as size increases, and the anomalous proportions for the hummingbirds. In figure 1, however, wing length for birds is in general greater per unit weight than for insects. Wing area, however, for the long-winged insects is considerably greater per unit weight than for the long-winged birds.

Figure 4 is an expansion of figure 3 for birds (excepting hummingbirds) with a differentiation in charting for selected bird families. We see that in general the birds of prey have the highest, ducks and gallinaceous birds the lowest, relative wing area. Aerial performance does not necessarily track relative wing area. Ducks, for example, are strong and competent fliers, making up for their small wing area by an unusually high wing-beat rate.



Note also that soaring birds, the albatross particularly, are not extraordinary in relative wing area, falling generally in line with the small passerines.

#### WING LENGTH AND WING AREA

Figure 5 shows the relationship for birds, figure 6 for insects. The birds fall into a very consistent pattern, but here the differences for soaring birds become more apparent. The albatross, for example, has a very long wing per unit area, as does the frigatebird and booby. This means simply that for soaring birds the wings are long and narrow, a condition essential for good aerodynamic stability, which does not require per se a large wing area.

In figure 6, the insects show their unusually large "scatter." We have models ranging from the long, narrow wing of the fruitflies and crane-flies to the broad stubby wings of the butterflies. The proportionality constant in the equation relating wing area with the square of the wing length varies through a factor of 5. For birds the variation is scarcely a factor of 2.

Figure 7 shows data for bats. One sees that these data are very self-consistent and that the constant of proportionality is quite close to that for birds. The flying model is similar, much more so than the appearance of the two classes of animals would lead one to expect.

#### WING SPREAD AND WING LENGTH

In virtually all ornithological handbooks the wing length as given is not the length of the whole wing, but that of what is called the "hand," viz, the distance from the wing tip to the first articulated joint. This practice arises out of the great difficulty in measuring total wing length or wing spread from bird skins, as compared with the relative ease of measuring the length of the "hand." Figure 8 shows Magnan's data on wing spread plotted against the measurements of the length of the "hand." It is essential here to use data from a single investigation since precise measurement of wing spread is greatly influenced by the technique of the particular observer. We see that the two hands average 62 percent of the wing spread. The "scatter" is not great, a tribute to Magnan's self-consistency.

#### WING AREA AND WING WEIGHT

In dimensional theory, the weight of the wing should be proportional to the cube of its length, or to the 1.5 power of its area. Figure 9 shows the relationship for insects and birds. We see that wing weight is proportional not to the 1.5 power, but to the 1.67 power of the wing area. Since we have previously shown wing area proportional to the square

of the wing length, we must conclude that wing *thickness* increases with the 1.34 power of the wing length and that the wings include a steadily increasing percentage of total weight as the size of the animal increases.

While we know little about the structural properties of bird and insect wings, it is reasonable to assume that if the thickness increased as the first power of the length, the angular deflection at the wing tip during, let us say, the downbeat would be constant. Since wing thickness actually increases as the 1.34 power of wing length, the angular deflection at the tip must decrease with increasing size (or weight) of the animal. This may be related to maintenance of aerodynamic efficiency with increasing size, but the argument is certainly not an obvious one.

It is even more extraordinary to note that the data for insects and birds fall on a continuous straight line. The materials of which the wings are constructed are totally different for the two classes; a ribbed chitinous membrane for the former and a complex structure of bone, muscle, and feather for the latter. It must, however, follow that the mean density of wings remains the same quite regardless of the material of construction.

It follows from the wing area-wing weight relationship that the weight of the wings will comprise a steadily increasing percentage of total body weight as the size of the flying animal increases. For the mosquito *Aedes aegypti*, weighing 1 milligram, Sotavalta's data show 0.2 percent of the total weight contained in the wings, whereas for the falcon *Gyps fulvus*, weighing over 7 kilograms, the wings, according to Magnan, are 22 percent of total weight.

#### WING-BEAT RATE AND WING LENGTH

There is good evidence<sup>1</sup> that the beating of the wings of flying animals can be described using the well-known theory for mechanical oscillators. This theory presumes a resonance frequency for beating wings which will be maintained regardless of changes in either external or internal wing loading. It follows then that wing-beat rate will be constant for a particular animal. The equation is as follows:

$$f^2 = \frac{Kbr^2}{I}$$

where  $f$  is the wing-beat rate,  $br^2$  is proportional to the weight of the wing muscles, and  $I$  is the moment of inertia of the oscillating system, viz, the sum of the moment of inertia of the wings and the internal mo-

<sup>1</sup> Greenewalt, Crawford H., "The Wings of Insects and Birds as Mechanical Oscillators," Proc. Amer. Philos. Soc., vol. 104, No. 6, 1960.

ment of inertia of the wing muscles and whatever part of the skeleton vibrates with them. If we assume  $br^2$  proportional to  $l^3$  (or the weight of the animal) and  $I$  to  $l^5$  (the product of wing weight and the square of a distance proportional to wing length) we see that the product  $fl$  should be constant for a dimensionally similar series of animals. We have seen, however, from figure 9 that for the whole roster of flying animals the weight of the wing varies with the 3.3 power of the wing length. Hence it should follow that the constant will be proportional to  $fl^{1.15}$  not to  $fl$ .

In figure 10 we have plotted all available data for wing-beat rate against the corresponding wing length. We see that there is a limiting boundary line which does indeed have the slope 1.15. Unfortunately the data for birds are quite limited. I have obtained measurements for hummingbirds and for a few small passerines using high-speed cinematography, and Meinertzhagen gives data for a number of large birds whose wing frequencies are sufficiently low to permit visual counting. Even for insects there are insufficient data to show conclusively whether the slope 1.15 is characteristic also for particular families or genera of insects, or whether in these limited ranges a slope of 1.0 obtains. Figure 12 would appear to give some support to the latter hypothesis. Here we have placed the insects in four arbitrarily selected groups with decreasing values for  $fl$  assumed to be constant. It is seen that in quite general terms the various genera appear to fall on lines for which the slope is unity.

Whatever the proper exponent for  $l$  (and for a particular genus it makes little difference) the product  $fl$  appears to define the flying ability of the animal. This would place the fruitflies at the bottom of the list, with butterflies not much better. The best fliers would appear to include many of the Hymenoptera, certain Diptera genera, and a few Coleoptera. The birds in general seem to be more proficient fliers than the insects, with the hummingbirds at least equal to the best in both groups.

The hummingbirds again appear to be anomalous, but the data are not good enough to establish quantitative relationships with sufficient precision. Figure 11 is an expansion of the hummingbird region. The best fit for the data appears to be a line whose slope is 1.25 and this slope correlates well with what one would expect from the other dimensional relationships for the family.

It is to be hoped that many more data for birds will become available in order that these relationships can be more precisely established. Ideally, of course, one should have data on wing length, wing weight, muscle weight, and wing-beat rate for each specific individual. Here

we have had to assume muscle weight proportional to body weight, which is true only in the most general terms.

### MUSCLE WEIGHT

In figure 13 we show the weight of the large pectoral muscle plotted against total weight for birds. The large pectoral muscle powers the downbeat of the wings, and so is the prime source of energy for flight. We see that for the entire procession of birds, from a tiny kinglet to a mute swan, the large pectoral averages 15.5 percent of the body weight with very little "scatter" on either side of the mean.

In figure 14 the weight of the large pectoral muscle is plotted against the weight of the wing. Here the scatter is considerably greater and the wing weight increases with the 1.1 power of the muscle weight. Body weight, on the other hand, increases with the first power of muscle weight. The rationale here is based on the data presented in figure 9. We recall that wing weight increases more rapidly than body weight, and since muscle weight is directly proportional to body weight it must also increase more rapidly than the weight of the muscle.

Figure 15 shows the weight of the small pectoral muscle (which powers the upbeat) plotted against body weight. Here we find the same proportional relationship that existed for the large pectoral muscle, but a far greater scatter from the mean. In general the gallinaceous birds have relatively large small pectorals; for soaring birds and birds of prey the small pectoral is a much lower percentage of body weight. The explanation is not readily apparent. Gallinaceous birds are relatively poor fliers, but it is hard to say why this should be associated with a relatively large small pectoral.

In figure 16 the weights of the two pectoral muscles are plotted against each other. We see that on the average the large pectoral has 10 times the weight of the small pectoral. The scatter from the mean is considerable, owing of course to the variability in relative weight of the small pectoral muscle.

The relative muscle weights provide the best available evidence for the presumption that for ordinary birds power for flight is provided wholly by the downbeat of the wings. If we make the reasonable assumption that power output is proportional to the weight of the muscle we see that the small pectoral can provide no more than 10 percent of the power required for flight. Since power must be expended merely to lift the wings, the contribution of the small pectoral muscle to flight may well be considerably less than this percentage.

For hummingbirds the situation is quite different. Large and small pectorals account for 25 to 30 percent of total weight as compared with



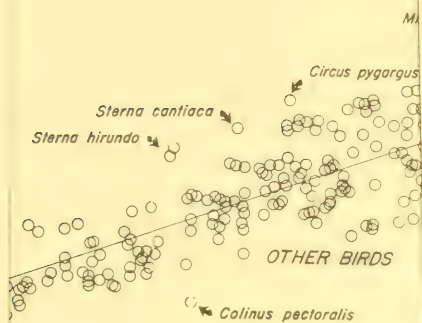
an average of 17 percent for ordinary birds. Hence one would expect hummingbirds to be relatively more powerful fliers. The ratio of the weights of the two muscles for hummingbirds is roughly 2 as compared with 10 for ordinary birds. One can then safely assume that both up-beat and downbeat contribute power for flight. This is also what one would expect from the pattern of the wing beat seen in high-speed moving pictures.

In figure 17, total muscle weight is plotted against body weight for insects. We see the usual scatter typical of dimensional data for insects. However, for many insects, notably the Neuroptera, Diptera, and Hymenoptera, total muscle weight is roughly the same percentage of body weight as is found for birds. For the butterflies, however, the musculature is very light, correlating with their poor flight performance.

Admittedly these same data could have been presented in many different ways. No attempt has been made, aside from figure 4, to subdivide the insects and birds into families and genera. Such an effort might well be fruitful, but the data collected here are probably not sufficiently precise to permit more than the broadest generalization. It is possible that relationships such as these will be of significance in taxonomic investigations both for insects and birds. It is to be hoped that someone will find the rather tedious investigations worth the effort.



WING LENGTH - millimeters



For Insects and Hummingbirds wing length is from wing tip to shoulder joint, for Other Birds length is one-half the wingspread.

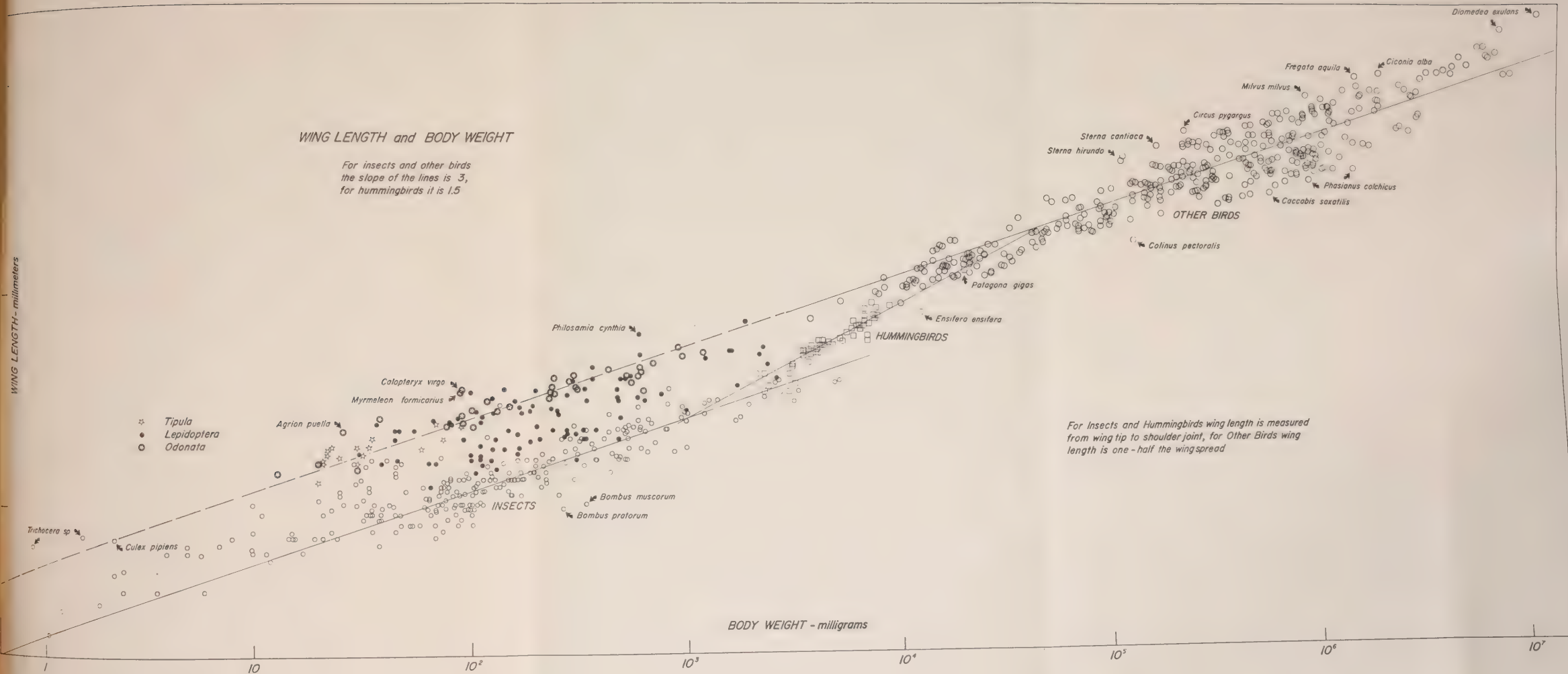




WING LENGTH - millimeters

# WING LENGTH and BODY WEIGHT

For insects and other birds  
the slope of the lines is 3,  
for hummingbirds it is 1.5



For Insects and Hummingbirds wing length is measured  
from wing tip to shoulder joint, for Other Birds wing  
length is one - half the wingspread

BODY WEIGHT - milligrams

FIG. 1



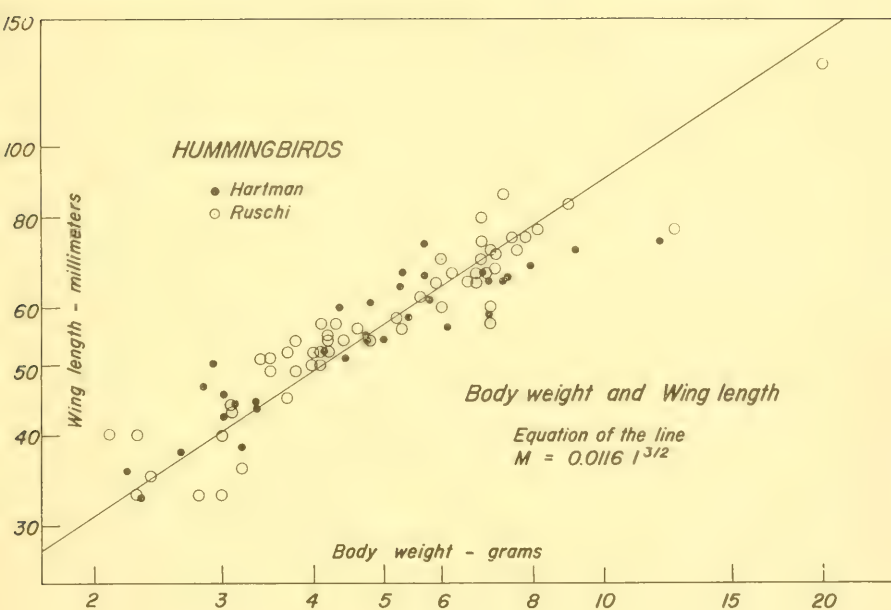


FIG. 2

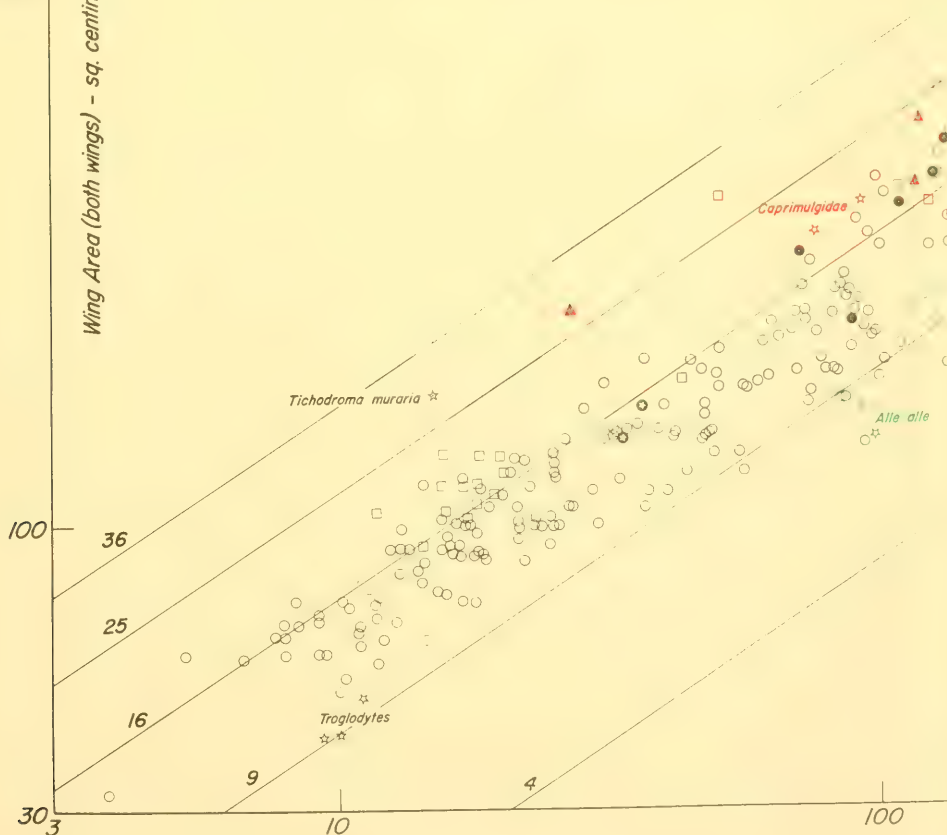




## WING AREA and TOTAL WEIGHT - BIRDS

If all birds were dimensionally similar, the wing area divided by the two-thirds power of the total weight would be constant. The plot shows this to be roughly the case for certain orders and families. Variations between families can, however, be very great. Ducks, for example, fall in a region for which "unit wing area" averages about 7.5, for falcons and allied genera, "unit wing area" averages about 20. Although precise data are not available, it is probable that ducks compensate for their relatively lower wing area with a correspondingly higher wing beat rate. "Unit wing area" is the constant in the equation  $A = cM^{2/3}$ . The lines in the plot correspond to the given values for  $c$ .

Wing Area (both wings) - sq. centimeters





# WING AREA and BODY WEIGHT

Wing area for all wings

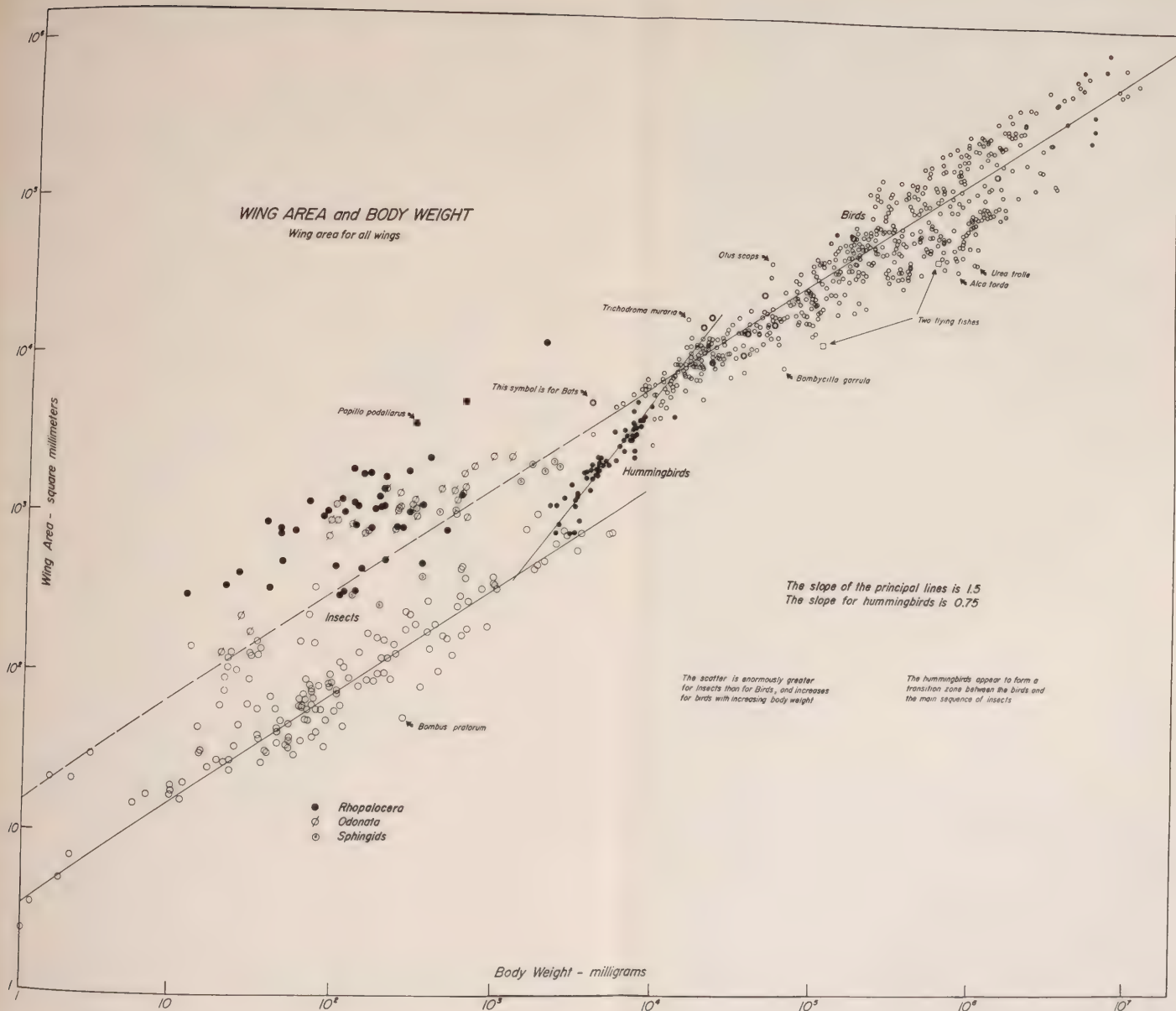


FIG. 3



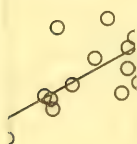
FIG. 4



100

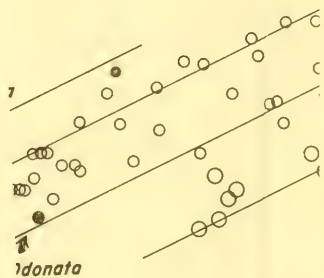
*Sula bassa*

*rbo* → ○

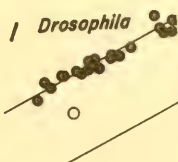


Wing Length - millimeters

10



EQUATION  
 $(length)^2$



1

1

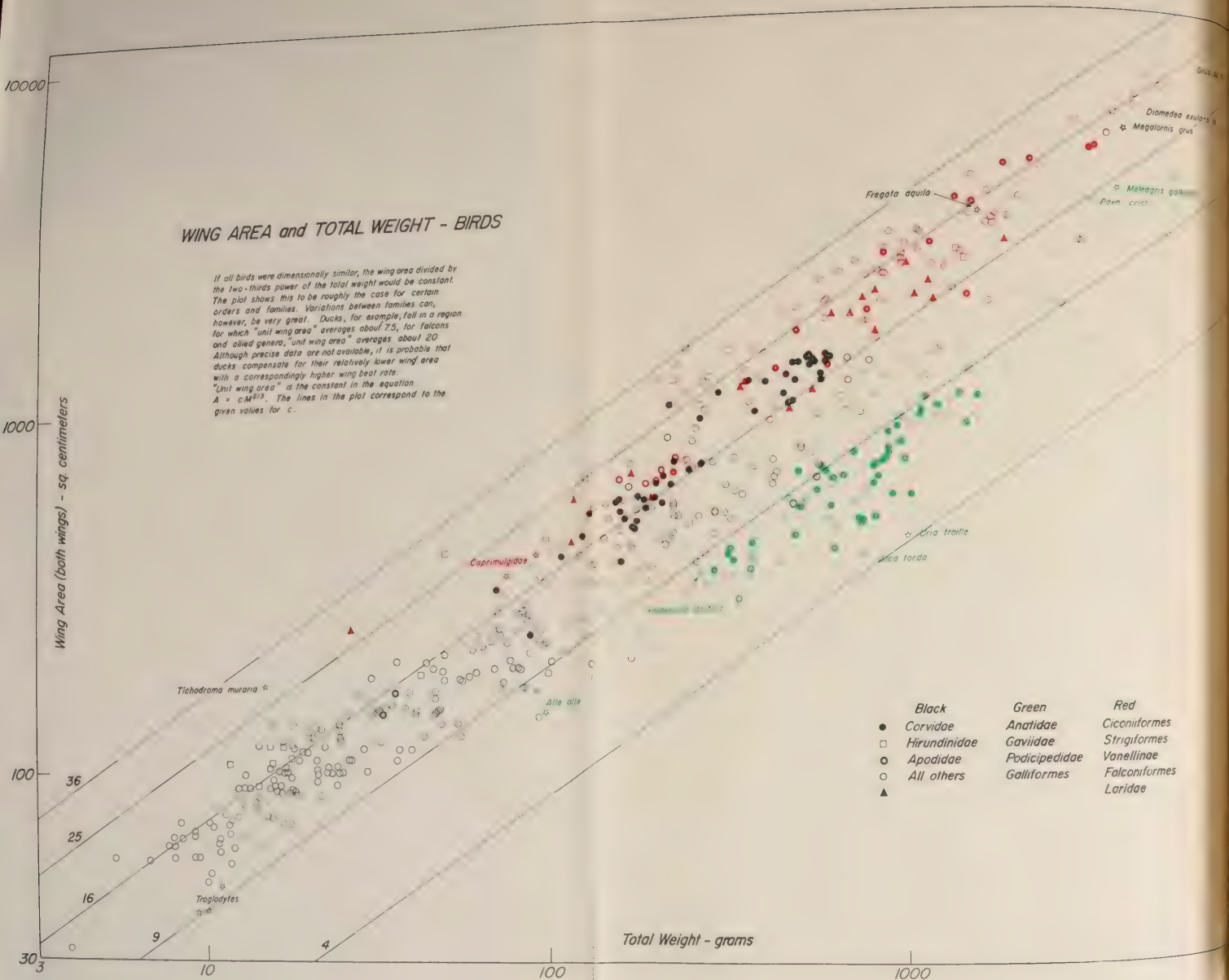


FIG. 4

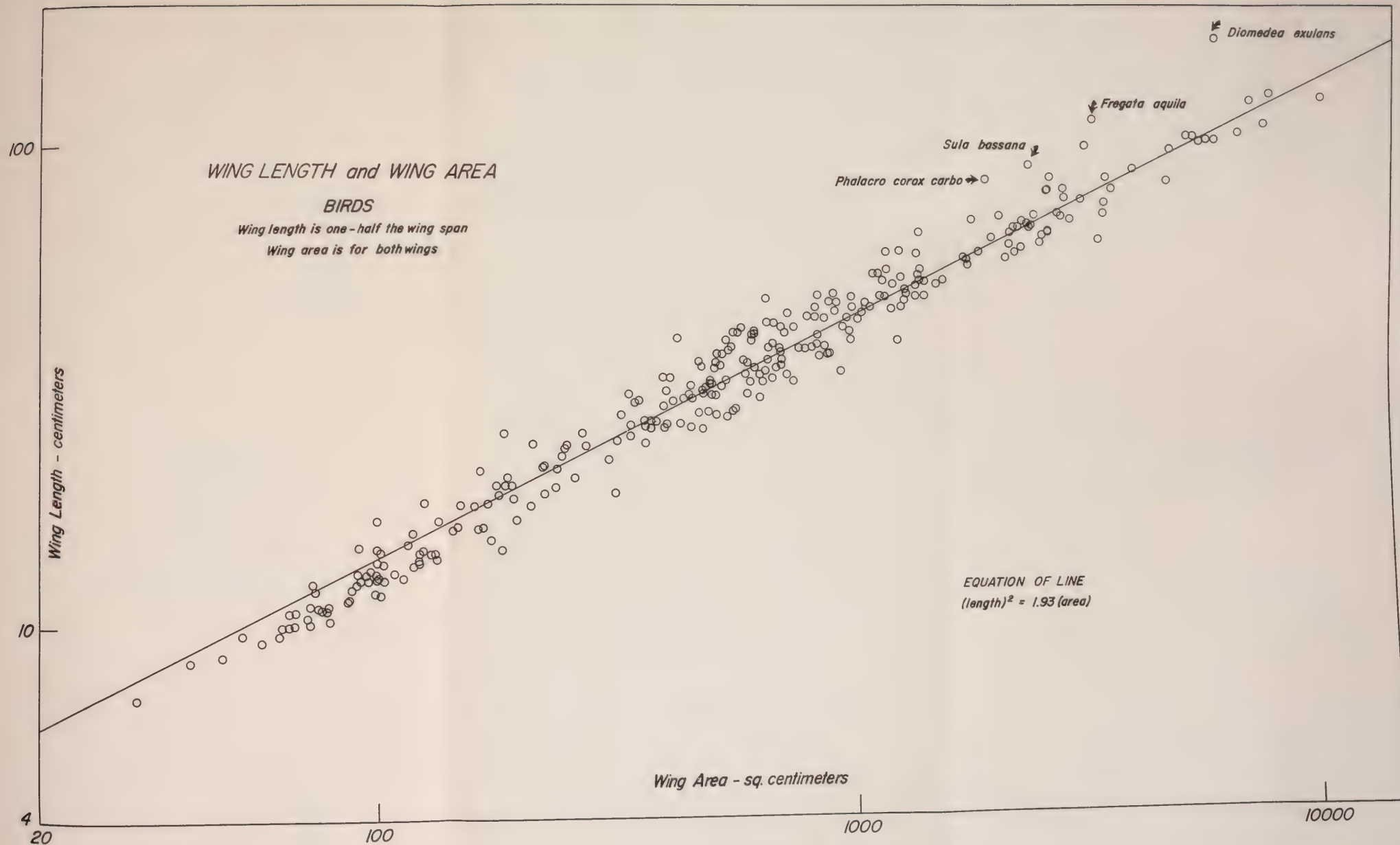
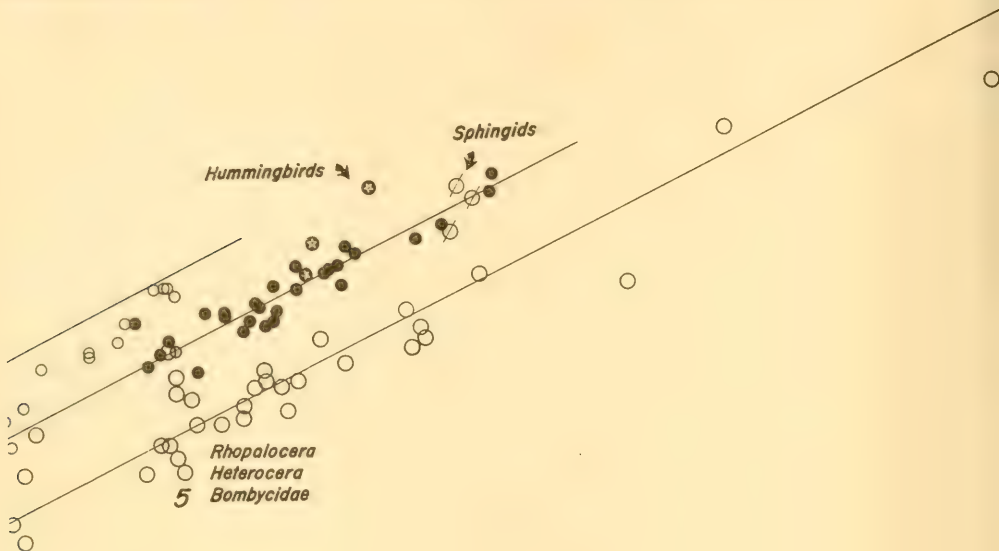


FIG. 5



General equation for all lines  
 $(length)^2 = c(area)$

Line	c
1	3.39
2	2.72
3	1.88
4	1.15
5	0.66

Narrow wings produce a high value for c  
 wide wings a low value

1000

10000



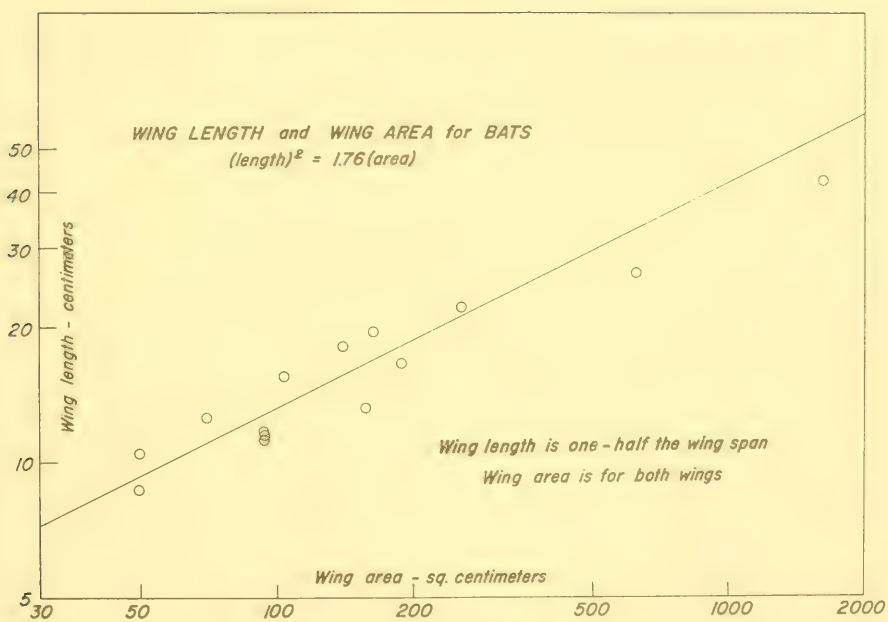


FIG. 7

100

# WING LENGTH and WING AREA

## INSECTS

Wing length is measured from wing tip to shoulder

Wing area is for all wings.

Wing Length - millimeters

10

1 *Drosophila*

3  
Diptera  
Hymenoptera  
Coleoptera

2 *Tipula*

4 *Odonata*

Hummingbirds

Sphingids

5  
*Rhopalocera*  
*Heterocera*  
*Bombycidae*

General equation for all lines  
 $(\text{length})^2 = c(\text{area})$

Line	c
1	3.39
2	2.72
3	1.88
4	1.15
5	0.66

Narrow wings produce a high value for c  
wide wings a low value

Wing Area - sq. millimeters

10

100

1000

10000

FIG. 6



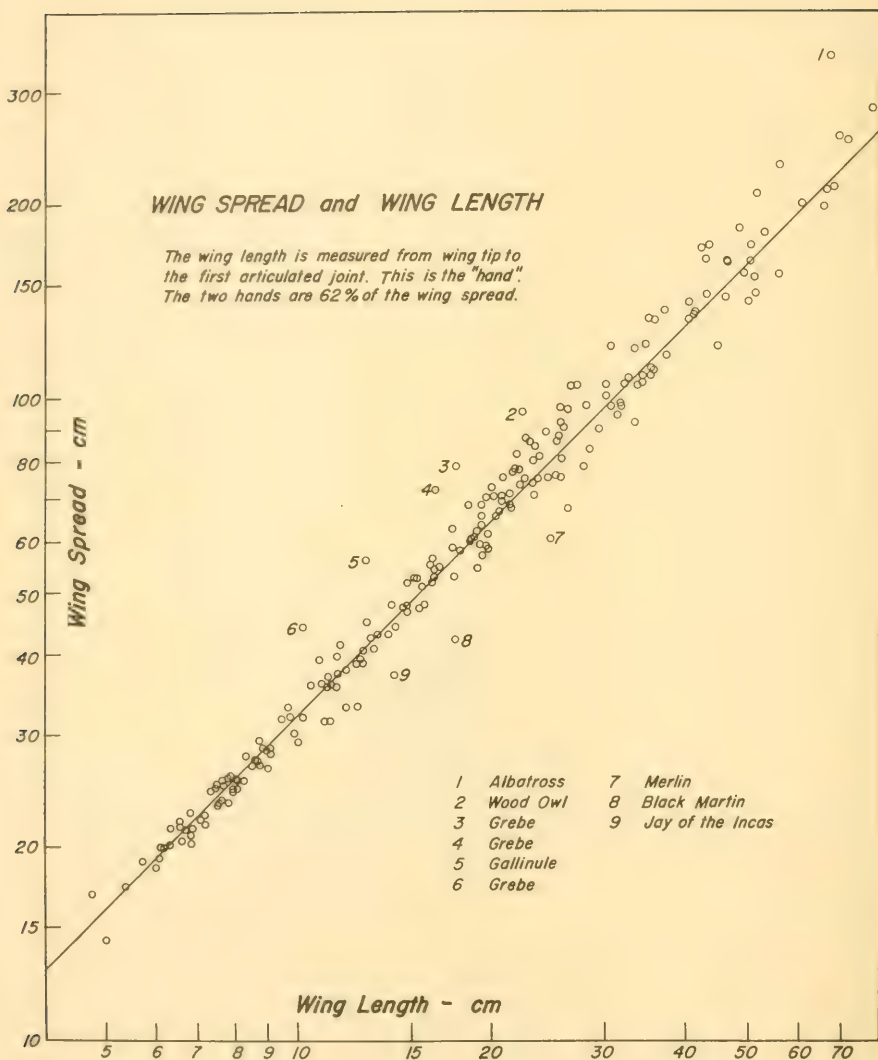
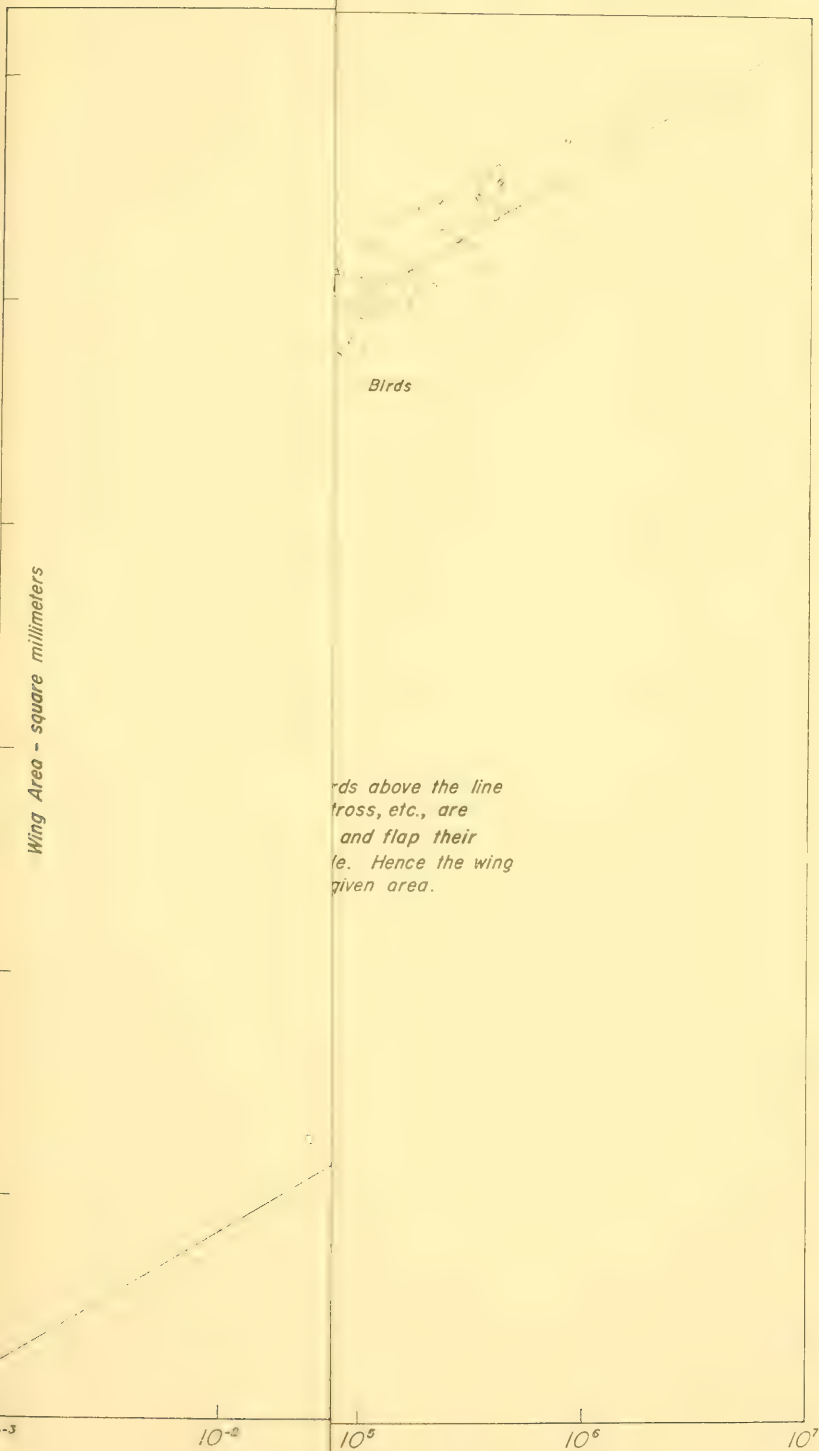


FIG. 8



Wing Area - square millimeters



birds above the line  
cross, etc., are  
and flap their  
fe. Hence the wing  
given area.



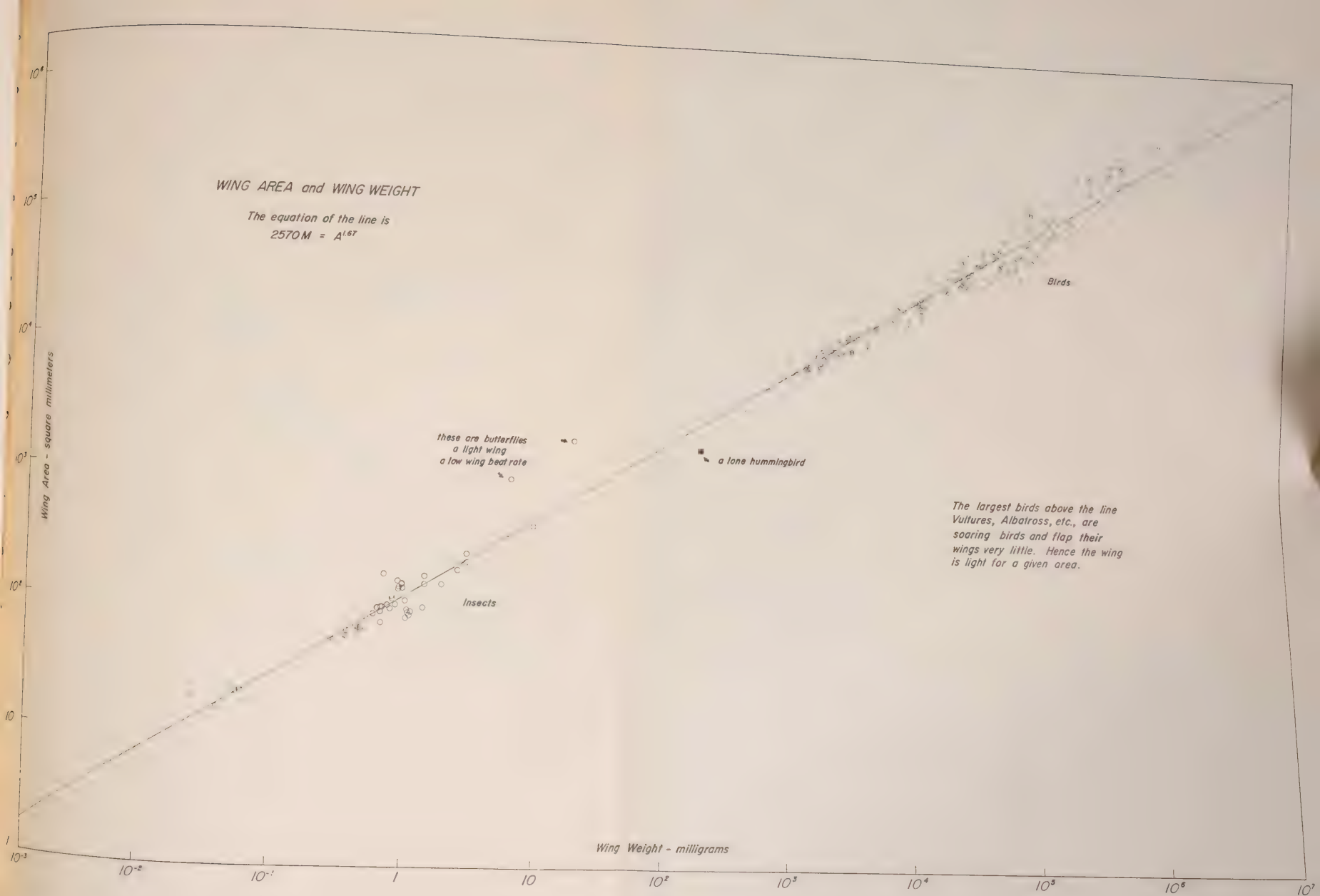


FIG. 9





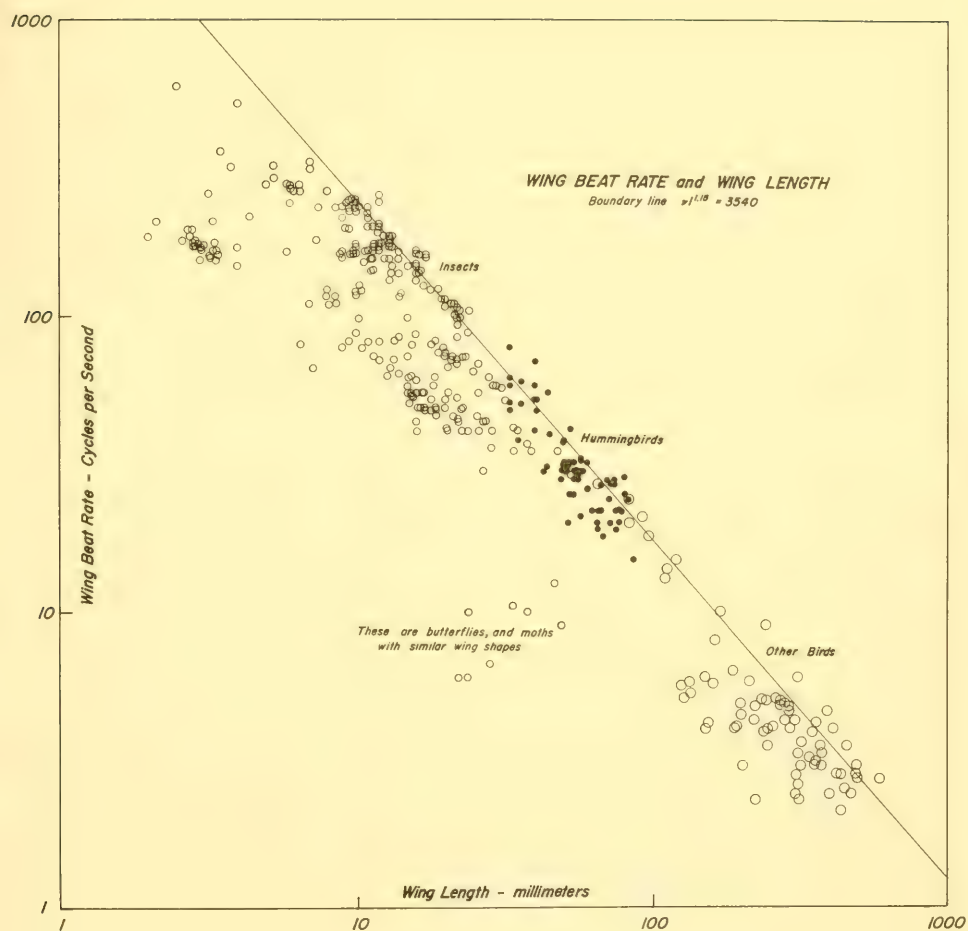


FIG. 10

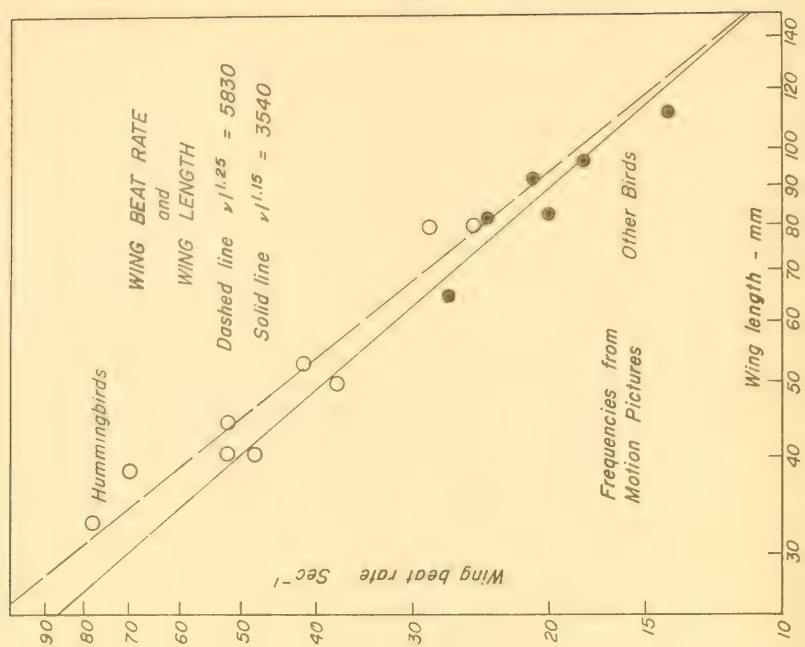
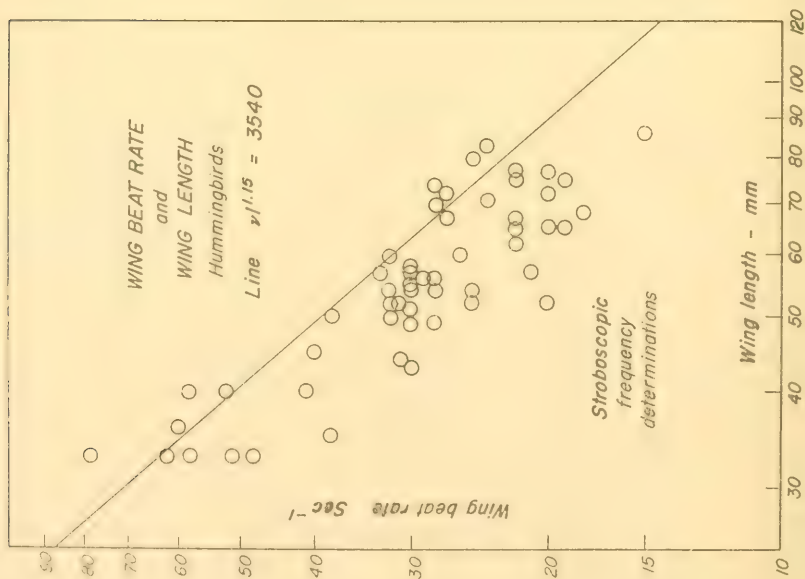


FIG. 11

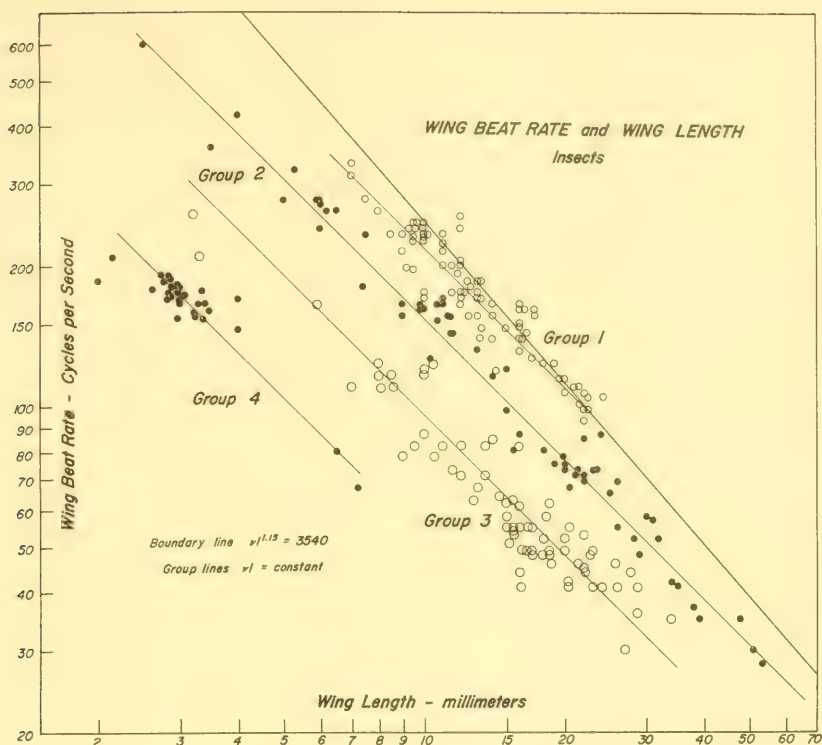


FIG. 12 —Wing-beat rate and wing length for insects

GROUP 1

HYMENOPTERA

ACULEATA

*Vespa*  
*Megachile*  
*Anthidium*  
*Psithyrus*  
*Bombus*  
*Apis*

COLEOPTERA

*Cetonia*  
*Potosia*

DIPTERA

NEMATOCERA  
*Chironomus*  
BRACHYCERA  
*Tabanus*  
*Neotamus*  
*Bombylius*  
*Volucella*  
*Eristalis*  
*Helophilus*

GROUP 2

LEPIDOPTERA

*Hemaris*  
*Chacrocampa*  
*Deilephila*  
*Sphinx*  
*Aegeria*  
*Cossus*

HYMENOPTERA

SYMPHYTA

*Trichiosoma*

*Sirex*

ACULEATA

*Camponotus*  
*Andrena*  
*Eucera*  
*Ammophila*

HEMIPTERA

ODONATA

*Aeschna*

COLEOPTERA

*Creophilus*  
*Amphimallon*  
*Melolontha*  
*Trichius*  
*Saperda*  
*Cerambycidae*  
*Macroglossum*  
*Geotrupes*

DIPTERA

NEMATOCERA  
*Aedes*  
*Culicidae*  
*Anopheles*  
*Theobaldia*  
BRACHYCERA  
*Calliphora*

GROUP 3

LEPIDOPTERA

*Acronycta*  
*Agrotis*  
*Sora*  
*Charax*  
*Hadena*  
*Hydroecia*  
*Xylina*  
*Poecilocampa*

HYMENOPTERA

SYMPHYTA

*Diprion*

ACULEATA

*Colletes*

TEREBRANTIA

*Amblyjoppa*  
*Colichneumon*  
*Opheltes*  
*Paniscus*  
*Eniscospilus*  
*Ophion*  
*Agrypon*

HEMIPTERA

ODONATA

*Sympetrum*

HETEROPTERA

*Mesocerus*  
*Carpocoris*  
*Dolycoris*

COLEOPTERA

*Aphodius*  
*Dermestes*  
*Pachyta*

BLATTARIA

*Periplaneta*

DIPTERA

NEMATOCERA  
*Tipula*  
*Pachyrrhina*  
*Limnobia*  
*Simulium*  
BRACHYCERA  
*Musca*  
*Chrysops*

GROUP 4

HYMENOPTERA

TEREBRANTIA

*Nemeritis*

DIPTERA

NEMATOCERA  
*Trichocera*  
BRACHYCERA  
*Drosophila*

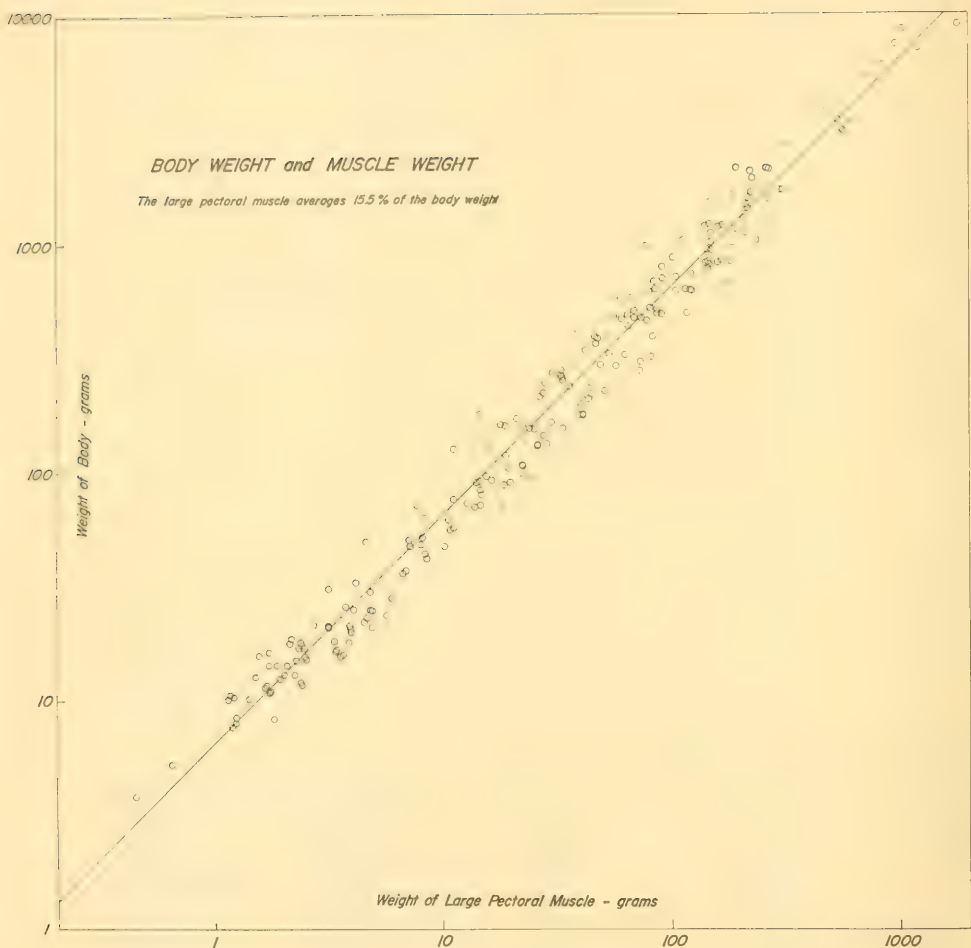


FIG. 13



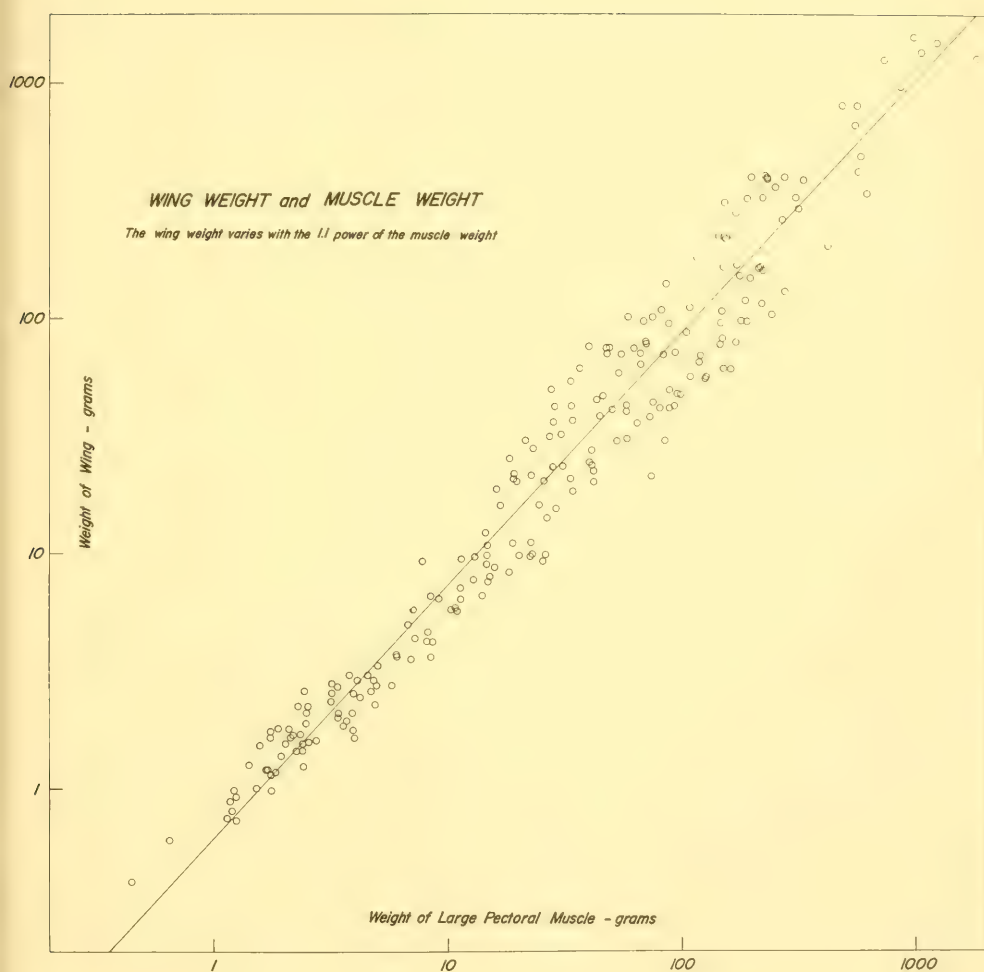
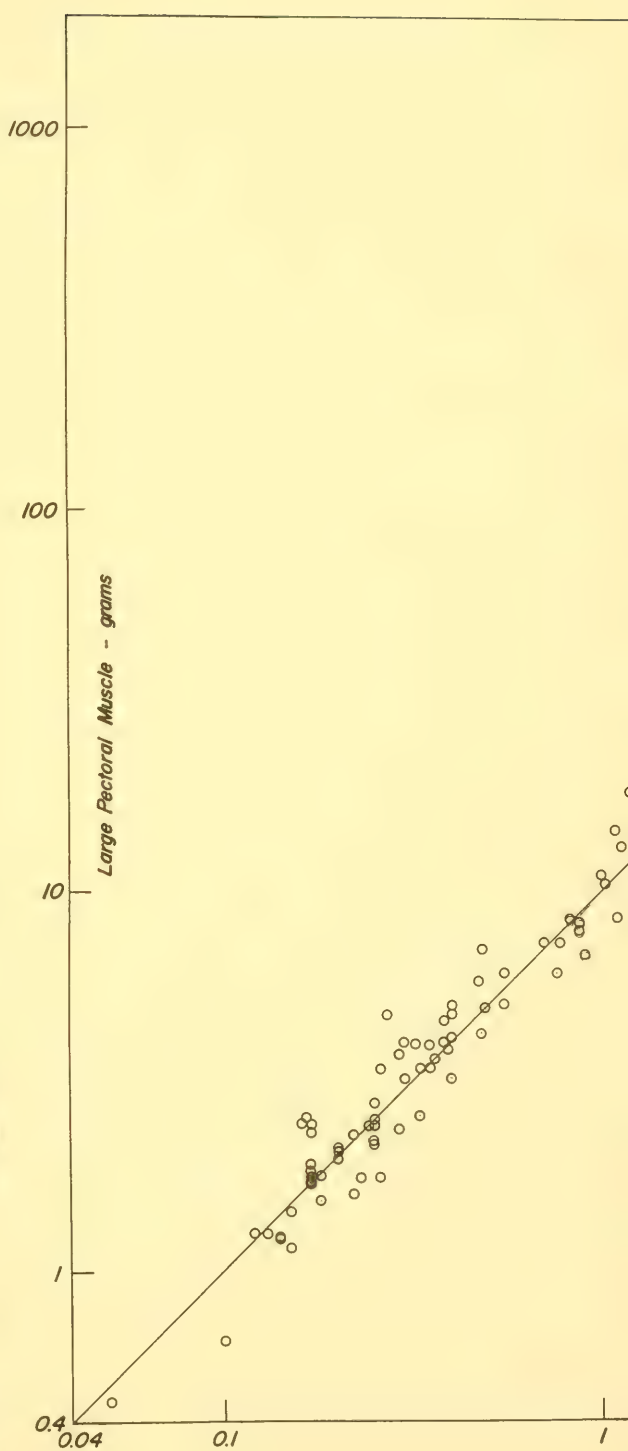
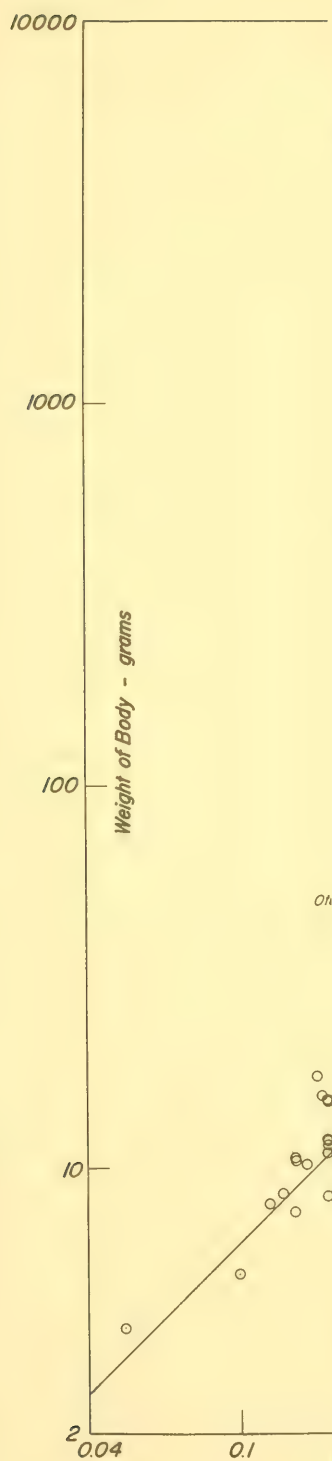


FIG. 14









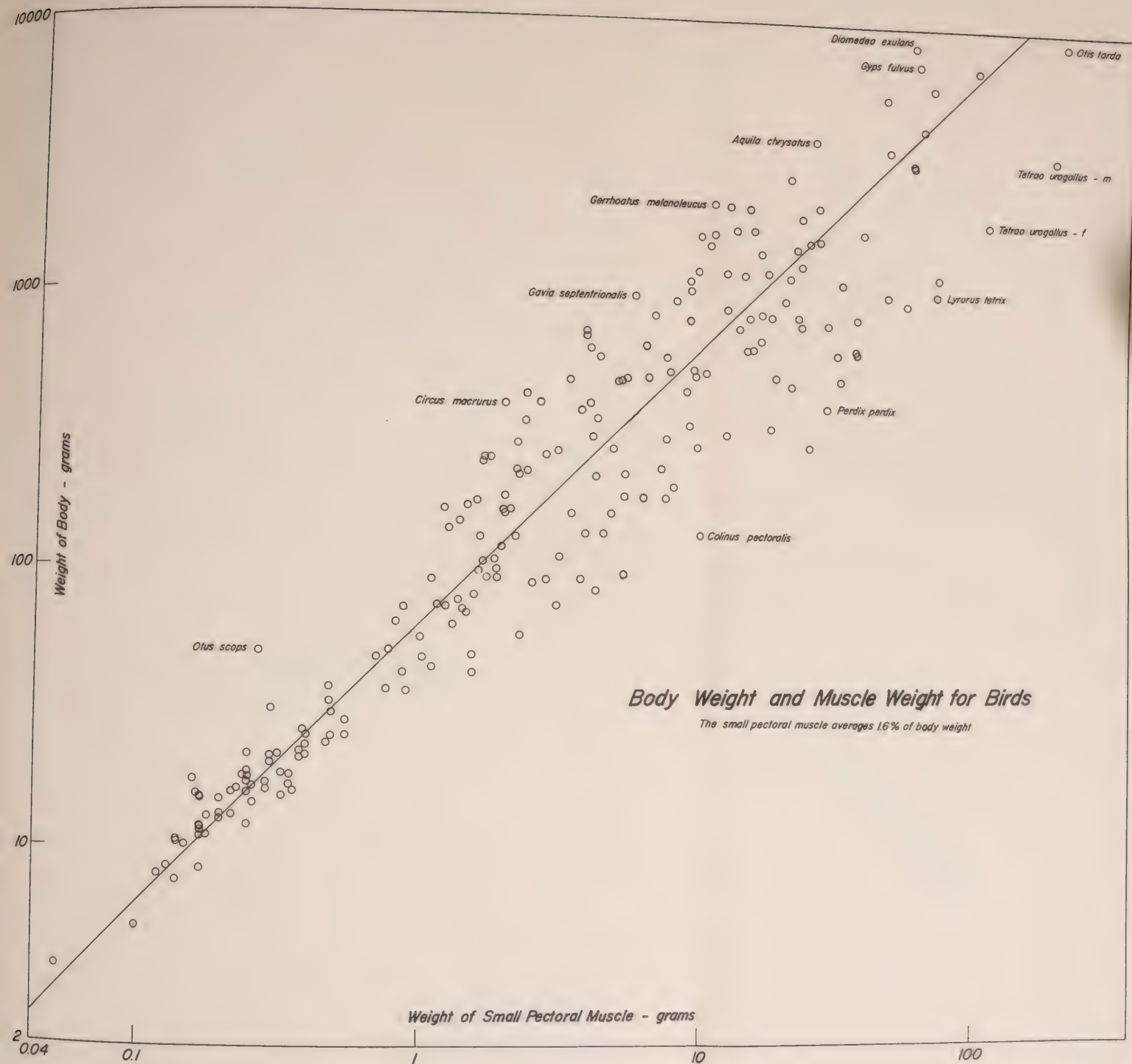
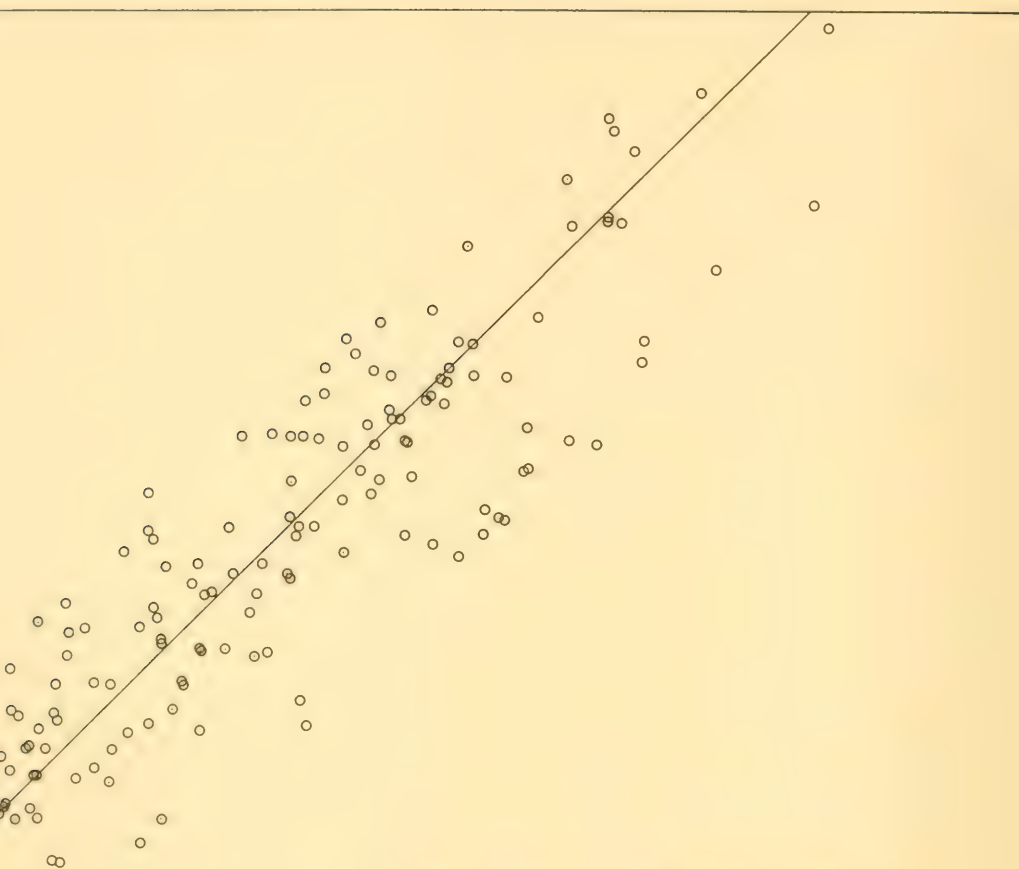


FIG. 15



*Large and Small Pectoral Muscles for Birds*

*The average ratio large to small muscle is 10*

*Small Pectoral Muscle - grams*

10

100

FIG. 16

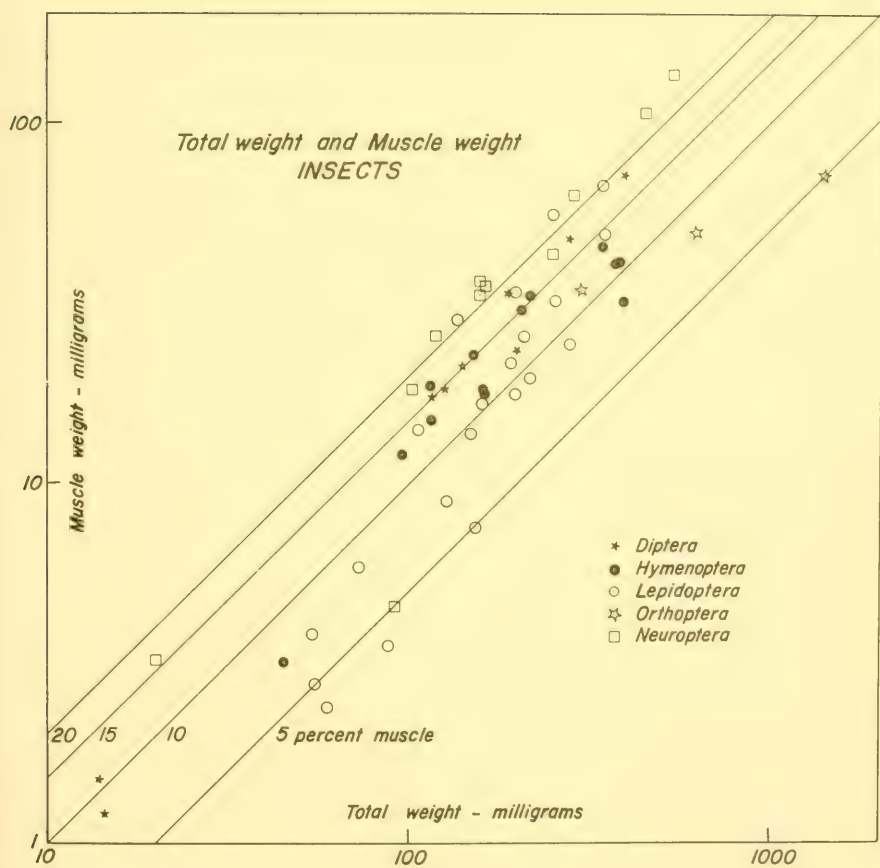


FIG. 17

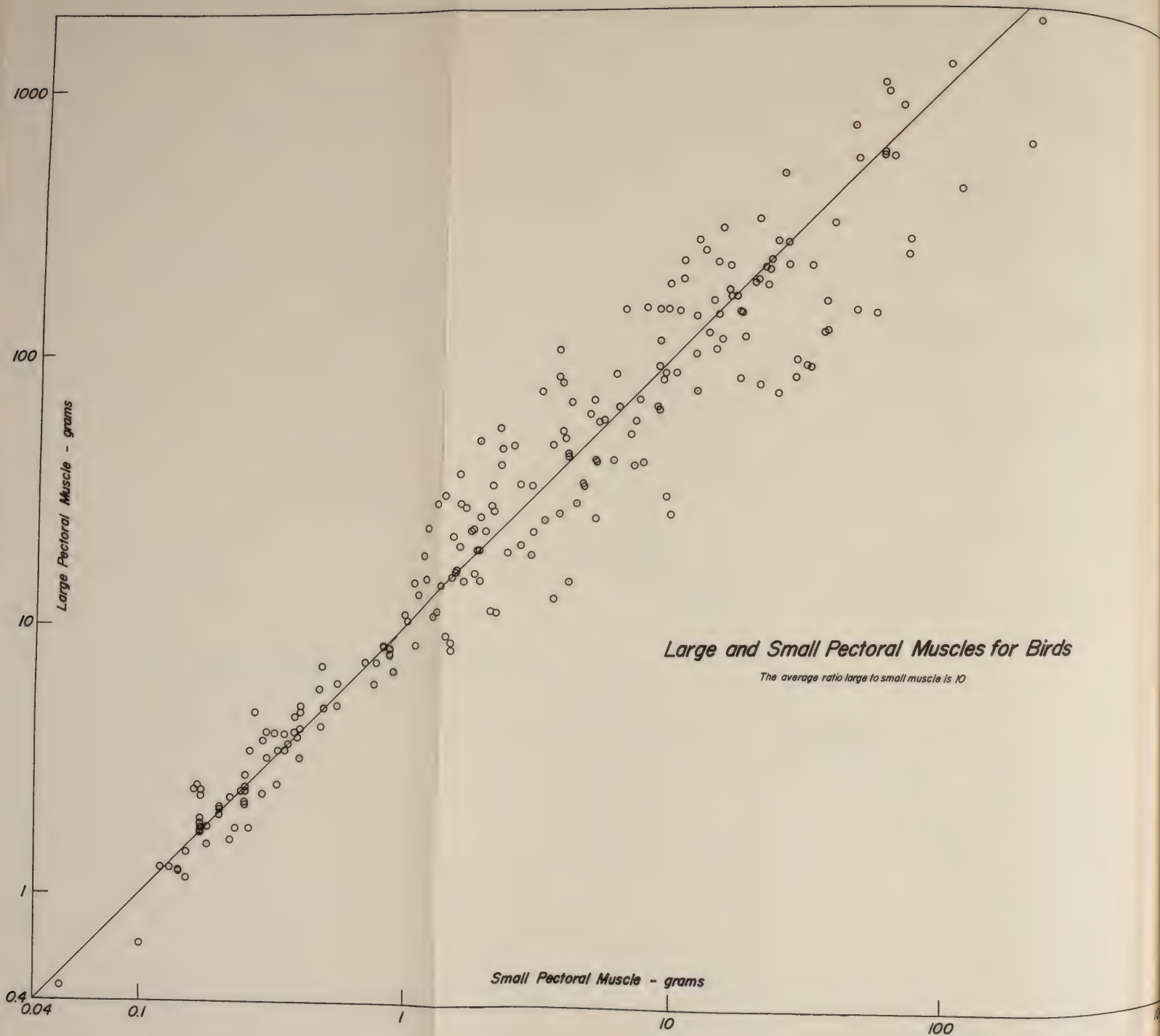


FIG. 16











METHODS EMPLOYED IN OBTAINING DATA FOR TABLES 1-3,  
FROM O. SOTAVALTA*Wing frequency:*

All papers—"Flight tone": Sotavalta has the gift of perfect pitch and made nearly all his measurements by the "acoustic" method. He reports a possible error in his determinations of -5 to +1 percent. Data are given which show his "acoustic" method to be in close agreement with direct stroboscopic measurements.

*Total weight:*

1947—Weights determined using "in most cases" a balance with a sensitivity of  $\pm 1$  mg. after exposure of the insect to HCN vapor for 10 to 15 seconds.

1952 } As above, but with a more accurate balance.  
1954 }

*Wing length:*

All papers—Measured using a common millimeter rule with an accuracy of  $\pm \frac{1}{2}$  to 1 mm. Distance is the "direct distance from the wing tip to the articular point."

*Wing area or total sustaining surface:*

1947—Measured by tracing the contour of the entire insect with spread wings on millimeter cross-section paper, "the wings then being fresh in their assumed striking position straight aside." This gives the "total sustaining surface."

1952—Measured as above but here the area of all wings alone was measured. This gives true "wing area" of all wings.

*Wing weight:*

1952—Weighings made on a microchemical balance with an accuracy of 1 microgram. For very small wings, several were weighed together and the average weight computed.

1954—As above but with a torsion microbalance of 5 micrograms sensitivity.

*Moment of inertia of wings:*

1952 } Determined by summation of the weights of small wing slices multiplied  
1954 } by the square of the distance of the slice from the articular point.





TABLE 1.—*continued*

	Wing- beat rate <i>sec-1</i>	Body weight <i>mg.</i>	Wing length <i>mm.</i>	Total sustaining surface <i>mm.<sup>2</sup></i>
HYMENOPTERA, Continued				
<i>Aculeata, Continued</i>				
<i>Megachile ligniseca</i> ♀ .....	233	115	10	...
“ <i>rotundata</i> ♀ .....	277	38	6.5	...
<i>Anthidium manicatum</i> ♂ .....	233	171	11	...
“ “ ♀ .....	233	90	8.5	...
“ “ ♀ .....	196	104	9.5	...
<i>Psithyrus rupestris</i> ♀ .....	123	541	18	361
“ <i>bohemicus</i> ♀ .....	123	715	19	...
<i>Bombus hortorum</i> ♂ .....	139	195	14	217
“ “ ♀ .....	131	533	16	262
“ “ ♀ .....	127	450	17	368
“ “ ♀ .....	147	337	15	...
“ <i>equestris</i> ♀ .....	262	58	8	...
“ <i>hypnorum</i> ♀ .....	150	485	16	...
“ “ ♀ .....	139	380	16	308
“ <i>agrorum</i> ♀ .....	170	225	13	192
“ <i>lapidarius</i> ♀ .....	165	537	16	284
“ “ ♀ .....	161	534	16	270
“ “ ♀ .....	161	487	16	...
“ <i>runderarius</i> ♀ .....	185	302	13	210
“ <i>pratorum</i> ♀ .....	233	101	9	90
“ <i>lucorum</i> ♀ .....	147	520	16	...
“ “ ♀ .....	161	487	16.5	...
<i>Apis mellifica</i> ♀ .....	233	85	9	86
“ “ ♀ .....	225	99	10	...
“ “ ♀ .....	225	97	9.5	...
“ “ ♀ .....	230	100	9.5	...
“ “ ♀ .....	230	99	10	...
“ “ ♀ .....	240	98	10	...
“ “ ♀ .....	247	94	9.5	...
“ “ ♀ .....	247	101	10	...
“ “ ♀ .....	214	65	9	...
“ “ ♀ .....	230	91	10	89
<i>Terebrantia</i>				
<i>Amblyjoppa proteus</i> .....	82	165	16	...
<i>Coelichneumon comitator</i> .....	123	32	10.5	...
<i>Opheltes glaucopterus</i> .....	52	95	20	...
“ “ .....	55	120	20.5	...
<i>Paniscus opaculus</i> .....	78	20	10.5	...
“ “ .....	78	22	10.5	...
“ “ .....	71	45	13.5	...
<i>Enicoospilus ramidulus</i> ♀ .....	73	25	11.5	...
“ “ <i>merdarius</i> ..	82	25	11	...
<i>Ophion luteus</i> .....	64	45	14	141
“ “ .....	55	45	15	...
“ “ .....	55	48	15.5	...
“ “ .....	55	35	16	...
<i>Agrypon anxium</i> .....	78	11	9	49
HEMIPTERA :				
<i>Heteroptera</i>				
<i>Mesocerus marginatus</i> .....	120	85	10	...
<i>Carpocoris purpureipennis</i> .....	117	74	10	...
<i>Dolycoris baccarum</i> ♂ .....	116	48	8	84

TABLE 1.—*continued*

	Wing- beat rate <i>sec-1</i>	Body weight <i>mg.</i>	Wing length <i>mm.</i>	Total sustaining surface <i>mm.<sup>2</sup></i>
HEMIPTERA, Continued				
<i>Odonata</i>				
<i>Aeschna juncea</i> .....	35	958	48	2,180
COLEOPTERA :				
<i>Creophilus maxillosus</i> .....	98	200	15	...
<i>Geotrupes stercorarius</i> .....	85	810	22	520
“ “ .....	87	1,000	24	684
“ “ .....	73	690	23.5	...
“ “ .....	73	540	23	...
<i>Aphodius subterraneus</i> .....	117	32	8.5	...
“ <i>finetarius</i> .....	82	35	9.5	...
<i>Amphimallon solstitialis</i> .....	75	364	19	...
“ “ .....	80	306	18	...
<i>Melolontha hippocastani</i> .....	58	1,220	29	965
<i>Trichius fasciatus</i> .....	116	170	14	...
<i>Cetonia aurata</i> .....	98	512	22	425
“ “ .....	107	478	22	...
“ “ .....	104	521	22.5	...
“ “ .....	101	437	21.5	...
“ “ .....	98	611	22.5	...
“ “ .....	114	323	19.5	...
“ “ .....	107	338	20	...
“ “ .....	93	478	22	...
<i>Potosia cuprea metallica</i> .....	110	521	21	...
“ “ .....	114	534	20	...
“ “ “ .....	110	529	21.5	...
<i>Dermestes lardarius</i> .....	110	21	7	...
<i>Pachyta quadrimaculata</i> .....	85	151	14	...
“ “ .....	82	126	13.5	...
“ “ .....	82	74	12	...
<i>Saperda carcharias</i> .....	55	1,010	26	...
“ “ .....	55	1,220	26	800
DIPTERA :				
<i>Brachycera</i>				
<i>Tabanus tropicus</i> ♀ .....	165	131	12	...
“ “ ♀ .....	185	81	13	...
“ “ ♀ .....	156	88	13	...
“ <i>bromius</i> ♀ .....	156	78	12.5	...
<i>Neotamius cyanurus</i> .....	170	42	10	...
<i>Bombylus maior</i> ♂ .....	255	60	12	...
“ “ ♀ .....	240	79	12	100
“ “ ♀ .....	230	36	10	65
“ “ ♀ .....	170	75	12	...
<i>Volucella pellucens</i> .....	147	200	15	...
“ “ .....	156	125	14	...
<i>Eristalis oestracea</i> .....	200	101	11	...
“ “ .....	200	83	11	...
“ “ .....	200	116	11.5	...
“ “ .....	200	104	12	...
“ “ .....	170	174	13	...
“ <i>tenax</i> .....	175	165	13	160
“ “ (same specimen) ...	161	150	13	160
“ “ “ “ “ .....	139	130	13	160

TABLE 1.—*concluded*

	Wing- beat rate <i>sec-1</i>	Body weight <i>mg.</i>	Wing length <i>mm.</i>	Total sustaining surface <i>mm.<sup>2</sup></i>
DIPTERA, Continued				
<i>Brachycera</i> , Continued				
<i>Helophilus trivittatus</i> .....	222	89	11	...
<i>Drosophila funebris</i> .....	170	6	4	...
<i>Nematocera</i>				
<i>Tipula excisa</i> ♂ .....	49	32	17	145
“ <i>lateralis</i> ♂ .....	67	32	13	75
“ <i>scripta</i> ♀ .....	52	59	18	...
“ <i>selene</i> ♀ .....	49	90	23	...
<i>Pachyrrhina analis</i> .....	62?	14?	18.5	...
“ <i>lineata</i> .....	87	10	10	...
<i>Limnobia quadrimaculata</i> .....	55	29	15.5	...
<i>Culicidae</i> sp. ♂ .....	523	2.5	4	10
“ “ ♀ .....	277	5	6	...
“ “ ♀ .....	277	2.5	5	...
“ “ ♀ .....	262	5	6.5	...
“ “ ♀ .....	270	5	6	...
<i>Anopheles maculipennis</i> ♀ .....	240	4	6	16
<i>Theobaldia alaskaensis</i> ♀ .....	233	10	7.5	...
<i>Chironomus plumosus</i> ♂ .....	311	13	7	24
“ “ ♂ .....	330	8	7	29
“ “ ♂ ( <i>s. sp.</i> ) ..	494	8	7	29

TABLE 2.—DATA FROM O. SOTAVALTA, ANN. ZOOL. SOC. "VANAMO,"  
VOL. 15, NO. 2 (1952)

	Wing- beat rate <i>sec-1</i>	Body weight <i>mg.</i>	Wing length <i>mm.</i>	Wing area <i>mm.<sup>2</sup></i>	Wing weight <i>mg.</i>	Moment of inertia of wings <i>mg. (mm.)<sup>2</sup></i>
LEPIDOPTERA:						
<i>Pieris brassicae</i> .....	10.5	144	34.0	1,720	17.975	4,230
" <i>napi</i> .....	6	37	23.6	853	5.975	698
<i>Macroglossum stellatarum</i> ..	73	282	21.3	379	9.180	593
<i>Poecilocampa populi</i> .....	55	112	16.7	317	5.225	265
HYMENOPTERA:						
<i>Aculeata</i>						
<i>Apis mellifica</i> .....	234	111	10.2	62.0	0.425	9.55
" " .....	247	84	9.7	57.6	0.425	7.32
" " .....	(240)	69	9.3	57.6	0.360	6.14
" " .....	(240)	77	9.6	57.9	0.365	6.92
<i>Bombus lapidarius</i> .....	143	477	16.6	172	2.465	131
" .....	(161)	658	17.3	189	2.745	169
" <i>terrestris</i> .....	156	880	17.3	197	2.860	158
<i>Vespa germanica</i> .....	139	240	16.2	133	1.390	69.6
" <i>vulgaris</i> .....	139	81	13.2	81.7	0.665	26.0
" " .....	147	98	13.3	85.2	0.760	27.8
" <i>crabro</i> .....	104	597	24.3	304	5.675	608
<i>Terebrantia</i>						
<i>Ophion luteus</i> .....	62	33	15.0	155	0.675	32.2
<i>Nemeritis canescens</i> .....	147	3.625	4.0	...	0.025	(0.061)
COLEOPTERA:						
<i>Melolontha vulgaris</i> .....	62	597	28.1	445	8.955	1,180
<i>Cerambycidae</i> sp. ....	80	142	15.5	133	1.845	68.8
<i>Amphimallon solstitialis</i> ....	78	291	19.9	229	2.840	187
DIPTERA:						
<i>Brachycera</i>						
<i>Calliphora erythrocephala</i> ....	143	...	11.4	85.9	0.605	14.9
" " .....	180	15	7.4	30.6	0.170	1.39
" " .....	156	94	11.3	79.6	1.030	18.2
" " .....	165	62	10.7	67.7	0.670	10.5
" " .....	156	106	11.4	73.1	1.000	17.4
" " .....	165	...	11.0	69.8	0.520	...
" " .....	161	61	9.8	61.1	0.460	7.33
" " .....	152	64	10.7	61.1	0.445	7.89
" " .....	...	...	9.3	50.5	0.275	4.37
" " .....	(161)	47	8.9	48.8	0.290	3.70
" " .....	127	...	10.3	67.6	0.375	...
" " .....	156	35	9.0	50.6	0.275	...
" " .....	165	33	9.0	52.5	0.360	...
" " .....	(161)	39	9.6	53.4	0.345	6.30
" " .....	161	30	10.0	57.0	0.430	...
" " .....	165	44	9.8	58.0	0.460	8.06
<i>Eristalis tenax</i> .....	175	50	11.5	67.3	0.655	15.9
" " .....	185	206	13.3	98.8	0.985	31.0
" " .....	175	106	12.2	76.5	1.050	23.8
" " .....	180	93	13.1	83.9	1.030	24.7
" " .....	156	...	12.5	81.1	0.645	...
" " .....	170	...	13.3	91.4	0.835	...
" " .....	185	176	13.0	87.9	1.355	27.6
" " .....	185	143	12.4	81.9	1.090	25.9
" " .....	191	...	11.8	76.9	1.045	24.2
<i>Musca domestica</i> .....	165	...	5.9	19.9	0.055	...



TABLE 2.—concluded

	Wing- beat rate <i>sec-1</i>	Body weight <i>mg.</i>	Wing length <i>mm.</i>	Wing area <i>mm.<sup>2</sup></i>	Wing weight <i>mg.</i>	Moment of inertia of wings <i>mg. (mm.)<sup>2</sup></i>
DIPTERA, Continued						
<i>Brachycera</i> , Continued						
<i>Drosophila melanogaster</i> ....	185	0.740	2.0	...	(0.0027)	(0.0017)
<i>Nematocera</i>						
<i>Tipula</i> sp. ....	63	21	15.5	75.5	0.460	29.0
" " .....	42	35	20.3	138	0.865	100
" " .....	63	30	15.5	87.9	0.655	44.1
" " .....	49	34	18.5	125	0.890	86.2
" " .....	49	30	18.5	130	0.930	83.2
" " .....	49	21	16.1	90.7	0.720	55.7
" " .....			16.9			
" " .....	63	20	12.7	61.4	0.465	13.9
" " .....	49	75	20.0	152	1.385	132
" " .....	48	23	18.5	131	0.930	71.4
" " .....	48	22	17.9	120	0.875	74.6
" " .....	48	22	17.0	106	0.785	51.5
" " .....	...	...	19.7	123	0.940	104
" " .....	49	25	16.5	101	0.785	54.3
<i>Trichocera</i> sp. ....	67	1.565	7.2	21.3	0.050	0.674
" " .....	80	0.830	6.5	18.0	0.025	(0.30)
<i>Theobaldia annulata</i> .....	262	9.900	6.2	16.9	0.065	60
" " .....	...	...	6.8	20.3	0.060	0.62
<i>Aedes aegypti</i> .....	600	1.025	2.5	2.4	(0.0022)	(0.003)
" " .....	360	1.890	3.5	5.0	(0.0080)	(0.020)
<i>Culicidae</i> sp. ♀ .....	277	5.800	5.9	15.0	0.040	(0.30)

TABLE 3.—DATA FROM O. SOTAVALTA, ANN. ENTOMOLOGICA FENNICA,  
VOL. 20, NO. 3 (1954)

	Wing- beat rate <i>sec-1</i>	Body weight <i>mg.</i>	Wing length <i>mm.</i>	Wing weight <i>mg.</i>	Moment of inertia of wings <i>mg. (mm.)<sup>2</sup></i>
LEPIDOPTERA :					
<i>Agrotis ypsilon</i> .....	58	169	18.2	5.235	325
" " .....	44	...	22.1	7.315	671
<i>Amphitrota clandestina</i> .....	44	150	22.0	6.730	654
" " .....	48	...	22.7	7.830	701
" " .....	46	...	21.3	5.845	428
<i>Sideridis unipuncta</i> .....	41	...	20.3	6.875	548
" " .....	46	111	18.6	3.025	233
<i>Amathes bicolorago</i> .....	54	69	15.5	2.645	138
" " .....	51	114	15.2	2.030	105
" " .....	53	64	15.6	2.225	99
" " .....	41	112	16.1	3.455	201
<i>Peocilocampa populi</i> .....	55	112	16.7	5.225	265
BLATTARIA :					
<i>Periplaneta americana</i> ♂ .....	36	820	28.8	25.8	2,590
" " ♂ .....	35	830	34.0	36.4	6,360
" " ♂ .....	32	...	...	...	...
ODONATA :					
			Fore	Hind	
<i>Sympetrum danae</i> ♂ .....	41	92	24.0	23.0	770
" " ♂ .....	44	101	27.5	26.5	1,550
" " ♂ .....	41	137	28.7	27.0	1,460
" " ♀ .....	41	102	23.0	22.0	590
" " ♂ .....	41	77	22.9	21.6	560
" " ♂ .....	46	90	25.8	25.0	720
" " ♂ .....	41	91	26.0	24.8	790

TABLE 4.—DATA FROM B. HOCKING, TRANS. ROY. ENTOMOLOGICAL SOC.,  
VOL. 104, PT. 8 (1953)

	Wing- beat rate <i>sec-1</i>	Wing area <i>mm.<sup>2</sup></i>	Wing length <i>mm.</i>
HYMENOPTERA :			
<i>Aculeata</i>			
<i>Apis</i> .....	198	28.3	9.2
DIPTERA :			
<i>Brachycera</i>			
<i>Tabanus affinis</i> .....	119	57.4	14.3
“ <i>septentrionalis</i> .....	98	29.3	10.2
<i>Chrysops furcata</i> .....	110	21.9	8.6
“ <i>nigripes</i> .....	109	18.9	8.1
<i>Drosophila</i> .....	208	1.5	2.14
<i>Nematocera</i>			
<i>Aedes campestris</i> .....	322	6.4	5.3
“ <i>communis</i> .....	216	3.9	4.4
“ <i>nearcticus</i> .....	318	3.6	3.8
“ <i>punctator</i> .....	290	6.4	5.3
<i>Simulium venustum</i> .....	258	3.8	3.2
“ <i>vittatum</i> .....	209	4.6	3.3

Hocking's paper is not clear as to whether the wing areas in the table above are for both wings or only one. In a recent letter he states that the measurements are for one wing and in the case of *Apis* for a pair of wings on one side.

TABLE 5.—DATA FROM REED, WILLIAMS, AND CHADWICK, GENETICS,  
VOL. 27, NO. 3 (1942)

	Wing- beat rate <i>sec-1</i>	Wing area <sup>*</sup> <i>mm.</i> <sup>2</sup>	Wing length <i>mm.</i>
<i>Drosophila immigrans</i> .....	166	3.19	3.40
“ <i>virilis</i> .....	156	3.39	3.23
“ <i>pseudoobscura</i> .....	191	2.31	2.83
“ “ .....	191	2.23	2.73
“ “ .....	175	2.48	2.84
“ “ .....	180	2.53	2.88
“ “ .....	173	2.63	2.88
“ “ .....	169	2.74	3.00
“ “ .....	166	2.82	3.00
“ “ .....	174	2.75	2.96
“ “ .....	179	2.60	2.98
“ “ .....	178	2.55	2.96
“ “ .....	182	2.56	2.96
“ <i>miranda</i> .....	173	2.93	3.09
“ “ .....	154	3.39	3.37
“ “ .....	159	3.29	3.21
“ “ .....	166	3.23	3.29
“ <i>athabasca</i> .....	154	2.72	2.96
“ <i>azteca</i> .....	188	2.43	2.86
“ “ .....	185	2.18	2.77
“ <i>repleta</i> .....	177	3.42	3.34
“ <i>funebis</i> .....	160	3.63	3.46
“ <i>melanogaster</i> .....	178	2.13	2.61
“ <i>duncani</i> .....	169	2.33	2.82

\* Both wings.

TABLE 6.—DATA FROM A. MAGNAN, LE VOL DES INSECTES, PARIS, 1934

	Weight mg.	Wing spread mm.	Wing length mm.	Wing surface mm. <sup>2</sup>	Wing weight mg.	Wing- beat rate sec-1
DIPTERA :						
<i>Culex pipiens</i> .....	2.25	10	4.8	21	—	—
<i>Tipula gigantea</i> .....	69	51	23.6	226	2.0	48
<i>Trichocere fuscata</i> .....	2.25	15.5	7.0	—	—	100
<i>Tabanus bovinus</i> .....	276	41	15.5	184	3.0	96
<i>Dasypamphus atra</i> .....	233	37	15.7	150	2.4	100
<i>Bombylius major</i> .....	45	22	9.0	44	0.4	—
<i>Chrysotoxum bicornutum</i> .....	75	28.5	12.8	68	1.0	120
" <i>vernale</i> .....	64	23.5	10.5	60	0.5	150
" <i>arcuatum</i> .....	73	28	12	74	0.6	144
<i>Volucella pellucens</i> .....	73	27.5	12	78	0.5	120
" <i>bombylans</i> .....	96	33	14	96	1.0	—
" <i>plumata</i> .....	124	32.5	13.0	92	1.2	120
" <i>zonaria</i> .....	215	40	17	124	3.0	—
" <i>inanis</i> .....	115	32	13	108	2.0	—
<i>Eristalis tenax</i> .....	73	28	11.5	74	0.6	210
<i>Echinomyia grossa</i> .....	197	34.5	14	124	2.0	—
<i>Catabomba pirastris</i> .....	34	27.5	12	40	0.4	190
<i>Sarcophaga carnaria</i> .....	45	19	7.5	36	0.45	160
<i>Calliphora vomitoria</i> .....	90	22	10	50	0.9	—
" <i>erythrocephala</i> .....	23	18	7.5	24	0.2	160
<i>Musca domestica</i> .....	12	13.5	5.5	20	0.2	190
<i>Fannia scalaris</i> .....	10	14	6	19.6	—	210
HYMENOPTERA :						
<i>Xylocopa violacea</i> .....	614	44	18	172	3.0	130
<i>Bombus lapidarius</i> .....	495	40	16.5	165	3.1	90
" <i>terrestris</i> .....	388	39	16	142	2.5	130
" <i>hortorum</i> .....	159	31	13	90	1.2	135
" <i>muscorum</i> .....	226	30.5	12.5	90	1.0	128
<i>Vespa crabro</i> ♀ .....	567	52.5	22.5	260	6.0	100
"    ♂ .....	373	40	18	180	2.4	—
" <i>germanica</i> .....	187	31	14	98	0.9	110
<i>Polistes gallicus</i> .....	115	26.5	11.5	46	0.6	220
<i>Apis mellifica</i> .....	78	20	8.5	42	0.5	250
<i>Ammophila sabulosa</i> .....	45	20	9	42	0.5	120
<i>Allantus tenuis</i> .....	52	—	11.4	—	—	70
LEPIDOPTERA :						
I. <i>Rhopalocera</i>						
<i>Papilio podalirius</i> .....	300	80	37	3,600	80	10
" <i>machaon</i> .....	370	82	38	2,200	45	—
<i>Pieris brassicae</i> .....	127	67	31	1,840	21	12
" <i>rapae</i> .....	87	52	25	1,000	8	—
" <i>napi</i> .....	55	49	22	760	5	—
<i>Anthocaris cardamines</i> .....	45	48	22	780	4.2	—
<i>Rhodocera rhamni</i> .....	107	61	27	1,200	12	21
<i>Vanessa urticae</i> .....	112	52	24	1,000	8	—
" <i>io</i> .....	195	62	28.5	1,400	17	18
" <i>levana</i> .....	131	45	20	820	8	—
" <i>atalanta</i> .....	134	57	27	1,080	15	10
" <i>cardui</i> .....	173	58	26.5	1,040	12	20
<i>Argynnis paphia</i> .....	160	66	30	1,760	18	—
" <i>pandora</i> .....	278	70	32	1,800	28	10
<i>Pararga moera</i> .....	67	53	24.5	1,160	7.2	—
" <i>megeoera</i> .....	45	44	20	720	3	—
<i>Coenonympha pamphilus</i> .....	46	37.5	16	480	3.5	22



TABLE 6.—continued

	Weight mg.	Wing spread mm.	Wing length mm.	Wing surface mm. <sup>2</sup>	Wing weight mg.	Wing- beat rate sec-1
II. Heterocera						
a. Sphingids:						
<i>Acherontia atropos</i> .....	1,600	110	51	2,050	67.0	22
<i>Sphinx convolvuli</i> .....	2,200	110	49	2,160	—	—
“ <i>ligustri</i> .....	2,400	104	44	2,000	—	—
<i>Macroglossa stellatarum</i> .....	345	47.0	20	400	10	85
“ <i>bombylififormis</i> .....	189	43.5	19.5	262	7.4	80
<i>Zygoena filipendulae</i> .....	127	38	18	300	5	48
b. Bombyces:						
<i>Callimorpha hera</i> .....	196	63	28	1,080	16.4	—
<i>Chelonia villica</i> .....	165	49	21	800	13.0	20
<i>Spilosoma fuliginosa</i> .....	106	36	14	300	3	—
“ <i>menthastri</i> .....	100	39.5	17	460	6	—
<i>Zeuzera aesculi</i> .....	340	51	20	480	15.6	—
<i>Dasichyra pudibunda</i> .....	237	62	27.5	800	13	28
<i>Bombyx rubi</i> .....	595	69.5	31	1,300	34	18
“ <i>quercus</i> .....	189	60	27	1,080	26.4	—
<i>Philosamia cynthia</i> .....	605	132	61	5,000	93	8
<i>Saturnia pyri</i> .....	1,890	150	70	12,000	300	8
<i>Notodonta dictaea</i> .....	201	52	23	500	8.4	22
<i>Pygoera bucephala</i> .....	257	58	26	800	18	—
c. Noctuids:						
<i>Agrostis exclamationis</i> .....	133	35	14.5	320	5	41
<i>Triphena promuba</i> .....	485	61	30	780	30	24
<i>Plusia gamma</i> .....	144	42	18	440	5	48
d. Phalenides:						
<i>Venilia macularia</i> .....	21	33.5	16	340	2.2	25
<i>Ephemera vulgata</i> .....	93	43	20	—	7	29
COLEOPTERA*:						
<i>Oryctes nasicornis</i> .....	2,700	87	37	744	34.6	—
<i>Lucanus cervus</i> .....	2,600	83	36	800	38.5	33
<i>Prionus cararius</i> .....	1,700	56	24	450	15	—
<i>Melolontha vulgaris</i> .....	961	62	28	402	12.8	46
<i>Cetonia aurata</i> .....	537	50	20	130	4	86
<i>Dorcus parallelipedus</i> .....	418	45	20	200	5	—
<i>Amphimallus fuscus</i> .....	201	39	16	160	4	—
<i>Cerambyx scopolii</i> .....	183	37.5	16	166	1.8?	—
<i>Telephorus fuscus</i> .....	109	28.5	12.5	116	1.6?	72
<i>Clerus alvearius</i> .....	71	24	11	82	1	—
<i>Aromia moschata</i> .....	133	31.6	14.3	—	—	—
ORTHOPTERA*:						
<i>Paracinema tricolor</i> .....	1,400	64	30	800	12.5	—
<i>Oedipoda coerulescens</i> .....	614	46	22	460	6.1	—
NEUROPTERA:						
<i>Libellules</i>						
<i>Sympetrum striolata</i> .....	232	61	31	780	8.8	—
“ <i>meridionale</i> .....	281	67	32	1,000	12.5	21
“ <i>fonsconlonbei</i> .....	157	61	29.5	760	8.2	—
“ <i>sanguineum</i> .....	101	58.5	28	860	6	—
<i>Leucorhinia caudalis</i> .....	237	68.5	33	1,020	9.8	—
<i>Libellula depressa</i> .....	245	80	38.5	1,320	14.4	20
<i>Orthetrum coerulescens</i> .....	248	65	32.5	1,080	14.6	20
“ <i>cancellatum</i> .....	303	80	39.5	1,200	18.9	—

\* For membranous wings only.

TABLE 6.—concluded

	Weight mg.	Wing spread mm.	Wing length mm.	Wing surface mm. <sup>2</sup>	Wing weight mg.	Wing- beat rate sec-1
EUROPTERA, Continued						
<i>Libellules</i> , Continued						
<i>Leptetrum 4 maculatum</i> .....	307	72	34.5	1,060	12.0	21
<i>Cordulia aenea</i> .....	201	71	33.5	—	9.6	33
<i>Gomphus vulgarissimus</i> .....	638	70	33.5	940	11.1	—
<i>Brachytron pratense</i> .....	557	77	36.5	1,200	14.4	33
<i>Ophiogomphus serpentinus</i> .....	312	71	34	940	12.8	42
<i>Anax formosus</i> .....	1,200	109	50	2,280	45.4	22
“ <i>parthenope</i> .....	703	94	45	1,950	27	—
<i>Aeschna rufescens</i> .....	611	90	43	1,780	31.2	20
“ <i>mixta</i> .....	530	80	39.5	1,380	21.5	38
<i>Calopteryx splendens</i> .....	120	64	30	—	11.8	16
“ <i>virgo</i> .....	91	70	34	880	5.2	—
<i>Pyrhosoma minimum</i> .....	38	49	25	—	2.0	27
<i>Ischnura elegans</i> .....	20	30.5	15.5	130	1.0	—
<i>Panorpa communis</i> .....	30	32	14.5	175	1.0	28
<i>Myrmeleon formicarius</i> .....	90	68.5	33	700	5	—

TABLE 7.—DATA FROM MAGNAN AND PERRILLIAT-BOTONET, C.R. ACAD.  
SCI., VOL. 195, PP. 559-561 (1932)

Weight of pectoral muscles and weight of body for insects

	Body weight mg.	Weight of muscle mg.	% Muscle weight
DIPTERA:			
<i>Musca domestica</i> .....	14	1.50	10.7
“ .....	14.5	1.20	8.27
<i>Volucella zonaria</i> .....	140	21.0	15.0
<i>Tabanus bovinus</i> .....	276.8	47.1	17.0
“ .....	393.4	70.9	18.0
<i>Echinomyia grossa</i> .....	197	23.3	11.8
<i>Gastrophilus equi</i> .....	115	17.3	15.0
<i>Eristalis tenax</i> .....	126.5	18.2	14.4
<i>Tabanus bovinus</i> .....	186	33.5	18.0
“ .....	183	33.5	18.3
HYMENOPTERA:			
<i>Bombus lapidarius</i> .....	149.5	22.4	15.0
“ .....	95	11.9	12.5
“ <i>hortorum</i> .....	159.5	17.9	11.2
<i>Vespa crabo</i> .....	373.4	40.0	10.7
“ .....	381	40.4	10.6
“ .....	389	31.5	8.1
<i>Bombus terrestris</i> .....	215.5	32.7	15.2
“ .....	205.5	30.0	14.6
“ <i>muscorum</i> .....	115	18.6	16.2
<i>Vespa crabo</i> .....	339	44.7	13.2
<i>Apis mellifica</i> .....	115	14.9	13.0
<i>Ammophila sabulosa</i> .....	45.2	3.17	7.0

TABLE 7.—concluded

## LEPIDOPTERA:

<i>Pieris brassicae</i> .....	127.3	8.82	7.0
“ <i>rapae</i> .....	87.7	3.51	4.0
“ <i>napi</i> .....	55.2	2.76	5.0
“ “ .....	59.5	2.38	4.0
“ “ .....	54.2	3.79	7.0
<i>Vanessa atalanta</i> .....	134	28.0	20.9
“ “ .....	249	54.8	22.0
<i>Macroglossa stellatarum</i> .....	345.5	48.4	14.0
<i>Callimorpha hera</i> .....	196.4	17.6	9.0
“ “ .....	157.5	16.5	10.5
“ “ .....	214.5	19.3	9.0
<i>Vanessa io</i> .....	195	33.6	17.2
<i>Rhodocera rhamni</i> .....	150.5	7.5	5.0
<i>Argynnis pandora</i> .....	250.5	31.6	12.6
“ “ .....	148.6	13.4	9.0
“ “ .....	206	25.4	12.3
“ “ .....	160	17.6	11.0
“ “ .....	278.5	24.2	8.7
<i>Plusia gamma</i> .....	72.5	5.80	8.0
<i>Spilosoma fuliginosa</i> .....	106.5	13.85	13.0
<i>Zeuzera aesculi</i> .....	340.7	76.0	22.3
<i>Bombyx quercus</i> .....	189.5	21.2	11.2

## ORTHOPTERA:

<i>Oedipoda caerulycens</i> .....	614	49.1	8.0
<i>Cetonia aurata</i> .....	297.5	33.4	11.2
<i>Paracinema tricolor</i> .....	1,403.5	70.0	5.0

## NEUROPTERA:

<i>Diplax sanguinea</i> .....	101	18.2	18.0
“ “ .....	156.5	33.0	20.0
“ “ .....	117.5	25.5	21.7
“ “ .....	161.5	35.5	22.0
“ <i>jonsconlombi</i> .....	157	36.1	23.0
<i>Myrmeleon formicaris</i> .....	90.5	4.52	5.0
<i>Diplax meridionalis</i> .....	281.6	61.9	22.0
<i>Ischnura elegans</i> .....	20	3.20	16.0
<i>Orthetrum caerulescens</i> .....	248.2	42.7	17.2
<i>Aeschna cyanea</i> .....	445	106.7	24.0
“ <i>mixta</i> .....	530.5	136	25.6

TABLE 8.—DATA FROM KARL MÜLLENHOFF, PFLUEGER'S ARCH.  
GESAMTE PHYSIOLOGIE, VOL. 35, PP. 407-453 (1885)

Data for birds, bats, and insects

P—Total weight in grams.

Weighings made to three significant figures on freshly killed animals.

p—Weight of flight muscles in grams.

F—Total sustaining surface in square centimeters (values not given in the tables which follow). Birds were placed on their back with wings and tail feathers extended as in flight and the entire contour traced on white paper. Parallel lines 1 centimeter apart were drawn on the figure and the area measured, taking the mean length between lines and summing the areas.

Insects were mounted on needles, the wings arranged as in flight. After drying the specimens, the contours were traced on millimeter cross-section paper and the individual square millimeters counted.

f—Area of both wings in square centimeters.

Determination as for sustaining surface.

The area for a given contour could be measured with an accuracy 1 to 1,000, but repeated measurements on a given bird, because of variable stretching of the wings, would deviate by as much as 1 in 100.

K—Wing spread in centimeters.

l—Length of both wings in centimeters.

These were taken directly from the contour drawings made for the determination of F and f. They are accurate to 1 part in 100.

The values given by other observers were selected by Müllenhoff on the basis of their accuracy and self-consistency. The different observers are identified in the second column as follows:

1, Müllenhoff	4, V. Ledenfeld	7, De Lucy
2, Harting	5, Marey	8, Pettigrew
3, Mouillard	6, Legal and Reichel	9, Krarup Hansen

		Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l
BATS:							
1	<i>Pteropus edulis</i> .....	2	1,380	117.6	1,630	120	104.4
2	“ <i>geoffroyi</i> .....	3	53	—	—	48.4	—
3	<i>Macroglossus minimus</i> .....	2	21.4	—	94	24.5	22.4
4	<i>Phyllostoma perspicillatum</i> .....	2	47.7	—	190	36.8	33.2
5	“ <i>spectrum</i> .....	2	164	—	626	59.9	52.8
6	<i>Megaderma trifolium</i> .....	2	52.1	—	164	44.8	39.0
7	<i>Glossophaga soricinus</i> .....	2	14.6	—	94	24.0	22.8
8	<i>Vespertilio pipistrellus</i> .....	2	5.6	0.35	50	23.5	21.0
9	“ <i>murinus</i> ♂ .....	4	20.9	—	180	—	—
10	“ “ .....	2	34.9	—	140	42.0	36.0
11	“ <i>pipistrellus</i> ....	1	3.703	—	49.59	19.75	17.45
12	<i>Plecotus auritus</i> .....	2	10.4	0.76	70	26.0	25.0
13	<i>Taphozous saccolaemus</i> ....	2	18.7	—	158	29.5	26.4
14	<i>Mormops</i> sp. ....	2	20.8	—	94	28.7	23.4

TABLE 8.—*continued*

		Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l
BATS, Continued							
15	<i>Nyctinomus aegyptiacus</i> ..	3	6	—	—	24.3	—
16	<i>Molossus longicaudatus</i> ....	2	33.5	—	104	35.2	31.0
17	<i>Noctilio unicolor</i> .....	2	44.5	—	254	46.2	44.0
FLYING FISH:							
308	<i>Dactylopterus volitans</i> .....	2	572	—	440	41	43
309	<i>Exocoetus evolans</i> .....	2	107	—	124	24	21
BIRDS:							
18	<i>Lanius excubitor</i> ♀ .....	4	31	—	144	—	—
19	<i>Turdus merula</i> .....	5	94.0	—	230	—	—
20	" " ♂ .....	2	88.8	19.05	212	—	32.0
21	" " .....	6	74	19.6	168	—	—
22	" <i>pilaris</i> .....	1	100	—	186	39	33
23	" " ♂ .....	2	103.4	23.3	202	—	34.4
24	<i>Saxicola oenanthe</i> .....	5	56.1	—	125	—	—
25	<i>Parus coeruleus</i> .....	2	9.1	—	28	—	18.0
26	" <i>major</i> .....	2	14.5	2.10	62	—	21.0
27	<i>Alauda cristata</i> .....	5	36.8	—	202	—	—
28	" " .....	3	34	—	—	30.5	—
29	" " ♂ .....	3	37	—	—	33.1	—
30	" <i>arvensis</i> .....	2	32.2	5.10	150	—	31.6
31	<i>Emberiza gubernatrix</i> .....	2	25.5	2.03	100	—	21.0
32	<i>Fringilla spinus</i> .....	2	10.1	—	50	—	19.0
33	" <i>cannabina</i> .....	6	19	5.18	55	—	—
34	<i>Petrocincla cyanea</i> .....	3	53	—	—	—	—
35	<i>Budytes flava</i> .....	3	20	—	—	27	—
36	<i>Passer domesticus</i> ♀ .....	4	28.33	—	76	—	—
37	" " ♂ .....	3	27	—	—	23	—
38	" " ♀ .....	3	25	—	—	22.6	—
39	" " .....	6	34	8.74	82	—	—
40	<i>Bombycilla garrula</i> .....	2	60.0	11.0	88	—	32
41	<i>Sturnus vulgaris</i> .....	5	78	—	202	—	—
42	" " .....	6	82.5	20.48	192	36.5	—
43	" " ♂ .....	2	86.4	16.45	170	—	33.4
44	" " .....	3	71	—	—	38.4	—
45	<i>Gracula religiosa</i> .....	2	161	17.2	376	—	52.0
46	<i>Corvus aegyptiacus</i> .....	3	395	—	—	84	—
47	" <i>corax</i> .....	3	615	—	—	107.5	—
48	" <i>cornix</i> .....	6	615	141	1,343	—	—
49	" " .....	6	615	151	1,280	—	—
50	" " .....	6	598	140	1,144	—	—
51	" " .....	6	595	131	1,286	—	—
52	" " .....	6	565	140	1,310	—	—
53	" " .....	6	557	115	1,260	78	—
54	" " .....	6	557	120	1,324	—	—
55	" " .....	6	547	129.7	1,324	—	—
56	" " .....	6	519	121	1,280	—	—
57	" " .....	6	498	103.9	1,003	—	—
58	" " .....	5	375	—	1,156	—	—
59	" " .....	6	493	108.4	—	—	—
60	" <i>frugilegus</i> .....	6	575	1,219	1,285	92	—
61	" " .....	6	419	89	1,144	—	—
62	" <i>corone</i> .....	6	507	109.6	1,144	—	—
63	" " .....	6	484	100.6	988	—	—



TABLE 8.—*continued*

		Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l
BIRDS, Continued							
64	<i>Corvus corone</i> .....	6	498	115.1	1,284	—	—
65	" .....	6	477	93.6	1,190	—	—
66	" <i>monedula</i> .....	6	230	54.06	700	—	—
67	" .....	6	225	55.0	601.4	—	—
68	" .....	6	204	53.3	610	60.0	—
69	" <i>pica</i> .....	6	202	48.96	560	55.5	—
70	" .....	6	190	35.3	522	—	—
71	" .....	5	179	42.02	482	51	—
72	" .....	5	275	—	690	—	—
73	" .....	6	212	—	540	—	—
74	<i>Nucifraga caryocatactes</i> ....	6	176	43.3	460	—	—
75	" .....	6	174	39.6	466	—	—
76	<i>Garrulus glandarius</i> .....	6	125	36.4	443	—	—
77	" .....	6	132	37.5	508	—	—
78	" .....	1	180	—	565	56	47.3
79	" .....	6	156	40.1	546	—	—
80	" .....	6	165	39.9	490	—	—
81	" .....	6	188	45.0	551	—	—
82	<i>Upupa epops</i> .....	5	49.1	—	329	—	—
83	" .....	3	62	—	—	43.0	—
84	<i>Cypselus apus</i> ♀ .....	4	33.5	—	144	—	—
85	" .....	3	33	—	—	37.6	—
86	<i>Hirundo rustica</i> .....	4	15.7	—	135	—	—
87	" .....	4	19.4	—	114	—	—
88	" .....	4	18	—	110	—	—
89	" .....	4	19.9	—	134	—	—
90	" .....	4	19.9	—	134	—	—
91	" .....	4	19.4	—	114	—	—
92	" <i>urbica</i> .....	5	18.0	—	120	—	—
93	<i>Cotyle rupestris</i> .....	3	16	—	—	31	—
94	<i>Caprimulgus</i> .....	3	62	—	—	50.9	—
95	<i>Ceryle maxima</i> .....	5	86.0	—	2.88	—	—
96	" .....	5	82.9	—	270	—	—
97	<i>Psittacus erithacus</i> .....	2	300	37.9	584	—	59.6
98	" .....	1	200	—	710	71	60
99	<i>Chrysotis amazonica</i> .....	1	300	—	895	73	63
100	<i>Ptyctolophus sulfureus</i> .....	2	250	23.9	544	—	60.6
100a	<i>Picus viridis</i> .....	6	101	28.08	408	—	—
101	<i>Alcedo ispida</i> ♀ .....	3	27	—	—	23.2	—
102	" .....	3	31	—	—	25	—
103	" .....	3	34	—	—	26.2	—
104	<i>Coracias garrula</i> .....	3	133	—	—	62.5	—
105	<i>Merops apiaster</i> .....	5	18.30	—	117	—	—
106	<i>Vultur cinereus</i> .....	5	1,535	—	3,233	—	—
107	" sp. ....	5	1,664	—	3,131	—	—
108	<i>Otogyys auricularis</i> .....	3	8,152	—	—	266	—
109	<i>Gyps fulvus</i> .....	3	7,501	—	—	251	—
110	<i>Neophron percnopterus</i> ....	3	1,705	—	—	161.5	—
111	<i>Haliaetus albicilla</i> .....	1	5,000	—	7,973	226	190
112	" .....	1	4,500	—	7,000	217	182
113	" .....	1	4,900	—	6,200	209	185
114	<i>Pandion haliaetos</i> .....	6	3,055	744	5,852	—	—
115	" .....	3	1,270	—	—	155	—
116	" .....	6	1,950	518	3,142	—	—
117	<i>Falco migrans</i> .....	5	620	—	1,904	—	—

TABLE 8.—*continued*

		Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l
BIRDS, Continued							
118	<i>Falco tinnunculus</i> .....	5	129	—	642	—	—
119	“ “ .....	3	181	—	—	74.0	—
120	“ “ .....	6	260	51.7	680	65	—
121	“ “ minor .....	5	147	—	546	—	—
122	“ kobeck (?) .....	5	282	—	970	—	—
123	“ subbuteo .....	5	510	—	1,684	—	—
124	“ peregrinus .....	3	580	—	—	104	—
125	<i>Milvus aegyptius</i> .....	3	640	—	—	133	—
126	<i>Astur palumbarius</i> .....	1	800	—	1,520	103	92
127	“ “ .....	3	290	—	—	71.8	—
128	<i>Accipiter nisus</i> ♀ .....	1	260	—	800	75	67
129	“ “ juv. ....	6	275	85.1	690	68	—
130	“ “ .....	6	766	250	—	88.5	—
131	“ “ .....	3	152	—	—	61.8	—
132	“ “ .....	1	150	—	496	55.5	49.5
133	“ “ ♀ .....	1	250	—	710	69	60
134	“ “ ♂ .....	4	266	—	866	—	—
135	<i>Circus aeruginosus</i> .....	5	209	—	1,188	—	—
136	<i>Buteo vulgaris</i> .....	1	900	—	2,610	130	113
137	“ “ .....	1	900	—	2,590	126	109
138	“ “ .....	1	800	—	2,210	125	105
139	“ “ .....	1	600	—	2,170	117	100
140	“ “ .....	5	785	—	1,651	—	—
141	“ “ .....	6	785	154.6	—	—	—
142	“ “ .....	6	1,217	242	2,350	123	30.1
143	<i>Archibuteo lagopus</i> .....	6	862	176.9	2,280	120	—
144	“ “ .....	1	1,000	—	2,359	140	117
145	“ “ .....	1	890	—	2,020	129	108
146	“ “ .....	1	1,000	—	2,445	135	114
147	“ “ .....	1	1,000	—	2,510	144	123.5
148	“ “ .....	1	900	—	2,220	132	115.5
149	“ “ .....	1	1,125	—	2,880	143	123
150	“ “ .....	1	750	—	2,420	137	116
151	<i>Strix flammea</i> .....	1	400	—	1,190	97	84
152	“ “ .....	1	250	—	1,440	97	84.5
153	“ “ .....	3	305	—	—	94	—
154	<i>Asio otus</i> .....	1	275	—	1,010	92	88.5
155	“ “ .....	6	232	47.9	1,102	92	—
156	“ “ .....	6	237	50.84	1,154	—	—
157	<i>Asyo brachyotus</i> .....	1	370	—	1,230	103	88
158	<i>Syrnium aluco</i> .....	6	1,777	376	3,020	94.5	—
159	<i>Athene passerina</i> .....	5	129	—	442	—	—
160	“ “ .....	5	123	—	394	—	—
161	<i>Ephialtes scops</i> .....	3	150	—	—	52.6	—
162	<i>Columba livia</i> .....	7	290	—	750	—	—
163	“ “ ♂ .....	4	298	—	608	—	—
164	“ “ ♂ .....	1	205	—	598	70	59
165	“ “ ♀ .....	1	202	—	541	64	54
166	“ domestica .....	6	206	93.8	—	—	—
167	“ “ .....	6	335	113	650	64	—
168	“ aegyptiaca ♂ .....	3	257	—	—	56	—
169	“ vinacea .....	5	112	—	292	—	—
170	“ aegyptiaca .....	3	223	—	—	59.4	—
171	“ “ .....	3	110	—	—	21.5	—
172	<i>Tetrao urogallus</i> ♂ .....	1	2,700	—	1,785	116	96

TABLE 8.—continued

			Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l		
BIRDS, Continued										
173	<i>Tetrao urogallus</i>	♂	.....	1	2,600	—	1,800	113	96	
174	"	♀	.....	1	1,450	—	1,380	102	85	
175	"	tetrix	♂	.....	1	1,350	—	995	82	79.5
176	"	"	♂	.....	1	1,030	—	850	80	68
177	"	"	♂	.....	1	1,200	—	880	87	71
178	"	"	.....	1	730	—	530	62.5	51	
179	"	♀	.....	1	1,000	—	775	75	61.5	
180	"	bonasia	.....	1	370	—	340	52	40	
181	"	"	.....	1	375	—	375	51	40	
182	<i>Lagopus alpinus</i>	.....	.....	1	530	—	640	66	56	
183	"	"	.....	1	650	—	452	60	50	
184	<i>Perdix rufa</i>	.....	.....	1	380	—	400	51	41	
185	"	"	.....	1	340	—	340	49	38	
186	"	cinerea	♂	.....	1	450	—	365	53	41
187	"	"	.....	6	320	105	336	—	—	
188	"	"	.....	6	372	123	382	—	—	
189	"	"	.....	6	375	126	366	—	—	
190	"	"	.....	5	280	—	320	—	—	
191	<i>Coturnix communis</i>	.....	.....	3	100	—	—	—	—	
192	"	♂	.....	4	92.1	—	142	—	—	
193	<i>Pavo crist</i>	♂	.....	1	3,300	—	3,480	128	104	
194	<i>Phasianus colchicus</i>	♀	.....	1	950	—	755	64	52	
195	"	"	♂	.....	1	1,100	—	855	72	57
196	"	"	♂	.....	1	1,000	—	880	76	61
197	"	"	♂	.....	1	1,570	—	895	72	55
198	"	"	♂	.....	1	1,250	—	896	72	56
199	"	"	♂	.....	1	1,125	—	900	73	59
200	<i>Meleagris gallopavo</i>	.....	.....	3	3,000	—	—	110	—	
201	<i>Otis tarda</i>	♀	.....	1	8,900	—	5,729	207	184	
202	"	♂	.....	1	9,600	2,300	5,937	208	181	
203	<i>Grus</i>	.....	.....	7	9,500	—	8,543	—	—	
204	<i>Rallus pectoralis</i>	.....	.....	2	142	15.4	328	—	42.0	
205	"	aquaticus	♂	.....	2	170.5	19.05	202	—	33.0
206	"	"	.....	3	192	—	—	—	—	
207	<i>Fulica atra</i>	.....	.....	2	495	51.8	524	—	53	
208	<i>Gallinula chloropus</i>	.....	.....	3	595	—	—	69.6	—	
209	<i>Oedicnemus crepitans</i>	♀	.....	3	455	—	—	80	—	
210	"	♂	.....	3	470	—	—	77.3	—	
211	<i>Hoplopterus spinosus</i>	.....	.....	5	160	—	636	—	—	
212	"	"	.....	3	170	—	—	60.0	—	
213	<i>Charadrius pluvialis</i>	.....	.....	3	160	—	—	58.2	—	
214	"	"	.....	6	190	55.8	366	—	—	
215	"	"	.....	6	170	49.3	334	—	—	
216	"	minor	.....	6	59.5	17.6	183	—	—	
217	<i>Haematopus ostralegus</i>	.....	.....	6	555	137	722	81	—	
218	"	"	.....	6	488	79.5	—	75	—	
219	"	"	.....	6	521	128.1	740	—	—	
220	"	"	.....	6	445	106	642	—	—	
221	"	"	.....	6	437	99.4	697	—	—	
222	"	"	.....	6	389	93.9	670	—	—	
223	"	"	.....	6	358	42.1	562	—	—	
224	"	"	.....	6	341	84.8	708	—	—	
225	<i>Glareola torquata</i>	.....	.....	3	67	—	—	52.5	—	
226	"	"	.....	5	95.2	—	343	—	—	
227	<i>Vanellus cristatus</i>	.....	.....	6	190	53.5	614	—	—	

TABLE 8.—continued

		Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l
BIRDS, Continued							
228	<i>Vanellus cristatus</i> .....	6	204	55.0	624	—	—
229	“ “ .....	6	232	63.0	720	—	—
230	“ “ .....	6	232	64.4	730	66	—
231	“ “ .....	3	210	—	—	75.5	—
232	<i>Streptilas interpres</i> .....	6	136	32.7	235	—	—
233	<i>Scolopax rusticola</i> .....	1	300	—	500	63	53
234	“ “ .....	1	320	—	500	64	54
235	“ “ .....	1	300	—	505	63	53
236	“ <i>gallinago</i> .....	3	100	—	—	44.3	—
237	“ “ .....	1	300	—	440	59	48
238	“ “ .....	1	270	—	490	62	53
239	“ “ .....	1	300	—	505	60	51
240	“ “ .....	6	55	13.3	137	—	—
241	<i>Rhynchaea capensis</i> .....	3	103	—	—	40.6	—
242	<i>Numenius phaeopus</i> .....	2	440	59.3	964	—	90
243	“ <i>arquatus</i> ♂ .....	3	764	—	—	103	—
244	“ “ ♀ .....	3	520	—	—	95.5	—
245	“ .....	6	585	167	920	—	—
246	“ .....	6	615	175	—	—	—
247	“ .....	6	676	169	1,020	—	—
248	“ .....	6	695	199	936	93.5	—
249	“ .....	6	762	203	924	98	—
250	“ .....	6	898	217	1,160	—	—
251	<i>Machetes pugnax</i> ♂ .....	2	190	48.4	328	—	52.4
252	<i>Tringa cinclus</i> .....	6	120	31.5	262	—	—
253	“ <i>subarquata</i> .....	3	76	—	—	43.8	—
254	“ <i>canutus</i> .....	3	24	—	—	29.6	—
255	“ <i>sp.</i> .....	6	49.5	13.5	136	37	—
256	<i>Limosa rufa</i> .....	6	208	53.2	425	—	—
257	“ “ .....	6	220	56.2	428	—	—
258	“ “ .....	6	227	57.6	444	—	—
258a	“ “ .....	6	235	67.4	492	—	—
259	<i>Totanus sp.</i> .....	6	47	12.4	144	—	—
260	“ <i>sp.</i> .....	6	49	12.54	149.4	—	—
261	“ <i>fuscus</i> .....	6	229	58.6	494	—	—
262	<i>Recurvirostra avocetta</i> .....	3	325	—	—	70	—
263	<i>Ibis falcinellus</i> .....	3	365	—	—	90.0	—
264	<i>Ciconia</i> .....	6	3,300	857	4,880	170	—
265	“ <i>alba</i> .....	3	2,140	—	—	208	—
266	“ .....	7	2,265	—	4,506	—	—
267	<i>Ardea nycticorax</i> .....	3	615	—	—	104	—
268	“ <i>cinerea</i> ♀ .....	4	1,409.5	—	3,584	—	—
269	<i>Botaurus stellaris</i> ♂ .....	1	1,500	—	1,915	120	100
270	<i>Ardetta minutus</i> .....	3	318	—	—	89.3	—
271	<i>Anser cinereus</i> .....	3	2,020	—	—	137	—
272	<i>Anas</i> .....	6	606	165	642	78	—
273	“ <i>boschas</i> ♀ .....	1	880	—	685	83	69.5
274	“ “ ♂ .....	1	1,100	—	900	94	78
275	“ “ ♂ .....	1	900	—	710	83.5	70
276	“ “ ♀ .....	1	900	—	735	89	73
277	“ “ ♂ .....	1	950	—	838	87.5	75
278	“ “ ♀ .....	1	900	—	813	88	71
279	“ “ ♂ .....	1	1,000	—	687	85	72
280	“ <i>querquedula</i> .....	3	297	—	—	—	—
281	“ <i>crecca</i> ♂ .....	2	275.5	63.85	—	—	49.6

TABLE 8.—*continued*

		Ob- server	Weight <i>gms.</i> P	Flight muscles Wt.- <i>gms.</i> p	Wing area for both wings <i>cm.</i> <sup>2</sup> f	Wing spread <i>cm.</i> K	Length of both wings <i>cm.</i> l
BIRDS, Continued							
282	<i>Anas clypeata</i> ♂	3	925	—	—	72	—
283	“ “ ♀	3	727	—	—	70	—
284	<i>Fuligula cristata</i>	6	1,116	343	1,440	104	—
285	“ <i>clangula</i>	1	827	—	480	69	58
286	“ <i>glacialis</i>	1	922	—	550	74	63
287	“ <i>nyroca</i>	2	508	76.6	642	—	70
288	<i>Pelecanus onocrotalus</i>	3	6,625	—	—	280	—
289	<i>Procellaria gigantea</i>	3	2,880	—	—	175	—
290	<i>Puffinus kuhlii</i>	3	700	—	—	125	—
291	“ “	3	500	—	—	117	—
292	<i>Diomedea exulans</i>	8	12,700	—	—	400	—
293	<i>Larus melanocephalus</i>	3	232	—	—	94.6	—
294	“ “	3	280	—	—	96.5	—
295	“ <i>argentatus</i>	2	565	93.0	1,082	—	96
296	“ “	6	842	143	1,550	—	—
297	“ “	6	1,035	161.2	2,380	—	—
298	“ “	6	1,225	198	1,880	—	—
299	“ “	6	1,080	185	1,936	—	—
300	“ <i>ridibundus</i>	2	197	26.13	662	—	83.0
301	“ <i>canus</i>	6	355	68.3	1,118	108	—
302	“ “	6	642	—	1,748	—	—
303	“ “	6	720	130	1,742	—	—
304	“ “	6	785	130	1,920	—	—
305	<i>Sterna cantiaaca</i>	6	174	34.9	660	93.6	—
306	“ <i>hirundo</i>	6	116	25.3	427	79	—
307	“ <i>minuta</i>	6	53.0	11.9	185.4	50	—
INSECTS:							
311	<i>Ephemera vulgata</i>	1	30.8	—	126	37	34.5
312	<i>Calopteryx virgo</i> ♀	4	200	—	1,394	75	74
313	“ “ ♂	4	100	—	1,112	68	66
314	<i>Agriion puella</i> ♂	4	26	—	220	45	44
315	<i>Libellula cyanea</i> ♂	4	920	—	2,290	108	106
316	“ <i>depressa</i>	9	200	—	—	80	—
317	“ “ ♂	4	600	—	1,332	82	78
318	“ <i>vulgata</i> ♂	4	150	—	728	57	57
319	“ <i>cancellata</i> ♀	1	620	—	1,456	85	82
320	<i>Cordulia aenea</i> ♂	4	240	—	1,048	71	70
321	<i>Libellula cancellata</i> ♂	4	440	—	1,408	86	84
322	“ <i>quadrinaculata</i> ♂	4	290	—	1,108	76	74
323	<i>Setodes pilosus</i>	1	13	—	141	30	28
325	<i>Calosoma sycophanta</i>	1	641.4	—	390	54	43
326	“ “	1	802.6	—	336	57	44
327	<i>Hydrophilus piceus</i> ♂	1	5,212.4	—	779	88	74
328	“ “ ♀	1	4,950	—	770	85	72
329	“ “ ♂	1	3,327.6	—	674	79	66
330	“ “ ♀	1	3,175	—	600	72	59
331	<i>Dyticus marginalis</i> ♀ furrowed	1	1,777.2	—	479	60	50
332	<i>Dyticus marginalis</i> ♀ smooth	1	2,323	—	658	73	62
333	<i>Dyticus marginalis</i> ♀ furrowed	1	1,962	—	510	66	57
334	<i>Dyticus marginalis</i> ♂	1	1,277	—	600	70	60
335	<i>Acilius sulcatus</i> ♂	1	314.7	—	201	40	34



TABLE 8.—*continued*

	Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l
INSECTS, Continued						
336	<i>Colymbetes fuscus</i> .....	1	275.5	—	240	35
337	“ <i>grapii</i> .....	1	77	—	89	21
338	<i>Geotrupes stercorarius</i> .....	1	997.5	—	177	36
339	<i>Melolontha vulgaris</i> ♀ .....	1	950.8	—	366	50
340	“ “ ♂ .....	1	975	—	357	53
341	“ “ ♂ .....	1	667	—	285	49
342	<i>Ludius aeneus</i> .....	1	68.6	—	67	14
343	<i>Culex pipiens</i> .....	7	3	—	30	—
344	<i>Chironomus stercorarius</i> ..	1	1.2	—	3.5	6.5
345	<i>Pachyrhina pratensis</i> ♂ .....	1	41	—	69	32
346	“ “ ♀ .....	1	73	—	62	33
347	<i>Tabanus infuscatus</i> .....	4	160	—	176	—
348	<i>Leptis scolopacea</i> ♂ .....	1	29.5	—	62	25
349	“ “ ♂ .....	1	34	—	58	23
350	“ “ ♀ .....	1	78.2	—	58	23
351	“ “ ♂ .....	1	26	—	46	20
352	<i>Musca vomitoria</i> .....	1	65	—	72	18
353	“ <i>domestica</i> ♀ .....	1	16.9	—	25	12
354	“ “ .....	1	10	—	18	12
355	“ “ .....	1	11.5	—	16	12
356	<i>Pollenia rudis</i> .....	1	53.4	—	37	16
357	<i>Eristalis rupium</i> .....	1	88.2	—	34	16
358	“ <i>aeneus</i> .....	1	38.4	—	32	17
359	“ “ .....	1	38.7	—	31	18
360	“ “ .....	1	62.9	—	37	19
361	“ “ .....	1	35.5	—	27	15
362	“ “ .....	1	38.0	—	32	17
363	<i>Syrphus scriptus</i> .....	1	7	—	17	13
364	<i>Sarcophaga carnaria</i> .....	1	69	—	50	19
365	“ <i>stercoraria</i> .....	1	23	—	38	19
366	<i>Papilio podalirius</i> .....	1	340	—	1,120	68
367	<i>Pieris brassicae</i> .....	1	81.8	—	928	47
368	“ “ .....	7	200	—	1,660	—
369	<i>Rhodocera rhamni</i> ♂ .....	4	183	—	1,254	—
370	“ “ .....	1	128.4	—	1,138	53
371	<i>Argynnis aphirophoe</i> ♂ .....	4	25	—	404	—
372	<i>Vanessa urticae</i> .....	1	114	—	840	51
373	“ <i>C-album</i> .....	1	38.8	—	330	31
374	<i>Lycaena argus</i> ♂ .....	4	12	—	294	—
375	<i>Sphinx pinastri</i> ♂ .....	4	430	—	1,010	—
376	“ “ ♀ .....	—	—	—	—	—
	(with eggs) .....	4	540	—	1,030	—
377	<i>Sphinx ligustri</i> ♀ .....	4	1,920	—	1,864	—
378	“ “ ♂ .....	4	1,370	—	1,600	—
379	<i>Smerinthus ocellatus</i> ♂ .....	4	550	—	984	—
380	<i>Euplexia lucipara</i> ♀ .....	4	75	—	334	—
381	<i>Apis mellifica</i> ♀ .....	1	81.2	10	—	—
382	“ “ ♀ .....	1	80.2	12.4	—	—
383	“ “ ♀ .....	1	93.5	12.1	—	—
383a	“ “ ♀ .....	1	108.4	14.8	—	—
384	“ “ ♀ .....	—	—	—	—	—
	(with pollen) .....	1	103	—	57	16
385	<i>Apis mellifica</i> ♀ .....	1	74.2	—	39	15
386	<i>Bombus muscorum</i> .....	1	345.6	—	81	20
387	“ <i>pratensis</i> .....	1	443	—	103	28

TABLE 8.—concluded

		Ob- server	Weight gms. P	Flight muscles Wt.-gms. p	Wing area for both wings cm. <sup>2</sup> f	Wing spread cm. K	Length of both wings cm. l
INSECTS, Continued							
388	<i>Bombus pratorum</i>	1	271.2	—	52	26	19
389	"	1	257	—	90	26	22
390	<i>Systropha spiralis</i>	1	24.4	—	34	17	14
391	"	1	14.5	—	45	17	14
392	"	1	15.2	—	32	16	14
393	"	1	21.0	—	27	21	18
394	<i>Osmia bicornis</i>	1	52.9	—	47	21	16
395	" <i>adunca</i>	1	34.5	—	38	20	18
396	<i>Dichroa gibba</i>	1	19.2	—	28	16	14

TABLE 9.—DATA FROM AUGUSTO RUSCHI AND  
CRAWFORD H. GREENEWALT, UNPUBLISHED

Wing-beat rate, body weight, and wing length for certain hummingbirds.

The nomenclature is from Ruschi, derived, I believe, from Simon.

The wing-beat rates were measured, some by Ruschi, some by Greenewalt, using a portable stroboscope. In principle a slotted disk was fitted to a monocular so that the slotted portion of the disk passed through the optical axis. The disk was driven by a battery-operated variable-speed motor. A small generator, mounted on the shaft which carried the disk and driving motor, was connected to an ammeter calibrated in revolutions per second. The technique comprised sighting on a hovering bird and adjusting the motor speed until the wings appeared stationary. The wing-beat rate was read off from the ammeter connected to the generator.

The individual readings differ widely in probable error. In two cases—*Calliphlox amethystina* ♂ and *Melanotrochilus fuscus*—many readings were made and the observed rates are believed reliable to a few percent. For most of the others only one or two readings were possible, and the birds moved so rapidly that only a few seconds were available to bring the instrument to equilibrium. Individual readings could easily be in error by as much as plus or minus 10 percent.

Weights and wing lengths were obtained by Ruschi on the same individuals. These are not necessarily the same individuals for which wing-beat rates were determined.

For comparison, wing lengths, supplied by Lanyon, American Museum of Natural History, from the literature (principally Hartert), are also given.

The wing areas are calculated values. Length and area measurements are available for three species (*Archilochus colubris* and *A. alexandri* (Poole, 1938) and *Eupherusa eximia* (Magnan, 1922)). The averages for these three species result in the equation  $A = 0.71 l^2$  where  $l$  is the length in centimeters and  $A$  the area of both wings in square centimeters. The areas given in the table are calculated from Ruschi's wing-length measurements using this equation.

TABLE 9.—concluded

	Wing-beat rate sec-1	Weight of bird gm.	Wing area both wings cm. <sup>2</sup> calculated	Wing length mm.	
				Ruschi	Lanyon
<i>Melanotrochilus fuscus</i> .....	25	6.8	45.6	80	84.4
<i>Aphantochroa cirrochloris</i> .....	27	6.9	31.9	67	69.7
<i>Clytolaema rubricauda</i> ♂ .....	28	6.8	38.9	74	74.7
♀ .....	22	6.5	30.0	65	66.7
<i>Lophornis magnificus</i> ♂ .....	58	2.3	11.35	40	41
♀ .....	52	2.1	11.35	40	41
<i>Anthracothorax nigricollis</i> ♂ .....	28	6.8	34.8	70	69
<i>Eupetomena macroura macroura</i> .....	19	7.5	39.9	75	74.7
<i>Amazilia brevirostris</i> ♂ .....	38	4.0	17.8	50	50.7
<i>Colibri serrirostris</i> .....	28	6.0	34.8	70	74.7
<i>delphinae</i> .....	24	7.1	35.8	71	74.3
<i>coruscans</i> .....	24	8.9	49.0	83	80.3
<i>Boissonneaua jardini</i> .....	20	8.1	42.1	77	78
<i>Phaiolaema rubinoides aequatorialis</i> .....	20	6.7	30.0	65	72.7
<i>Hylocharis chrysura</i> .....	28	4.6	22.2	56	51.3
<i>Helianthus wilsoni</i> ♂ .....	18	7.1	32.8	68	72.7
<i>Hylocharis cyanus</i> ♀ .....	30	3.4	18.5	51	49.3
♂ .....	32	3.7	19.2	52	—
<i>sapphirina</i> ♂ .....	31	4.2	19.2	52	51.7
<i>Lophornis verreauxi</i> ♀ .....	41	3.0	11.35	40	44.7
<i>Calliphlox amethystina</i> ♂ .....	78	2.8	7.74	33	36
♀ .....	62	2.8	7.74	33	37
<i>Popelairia langsdorffi melanosternum</i> ♀ .....	51	3.0	7.74	33	37.3
<i>Ensifera ensifera</i> ♂ .....	22	12.5	42.1	77	80
<i>Florisuga mellivora</i> ♂ .....	27	6.2	31.9	67	69.7
<i>Popelairia langsdorffi melanosternum</i> ♂ .....	58	3.0	7.74	33	—
<i>Florisuga mellivora</i> ♀ .....	22	6.7	31.9	67	—
<i>Chrysolampis mosquitus</i> ♂ .....	30	4.1	23.1	57	56.3
<i>Chlorostilbon aureoventris</i> ♂ .....	30	3.5	17.0	49	50
<i>Stephanoxis lalandi</i> ♂ .....	25	4.2	20.7	54	52
♀ .....	20	4.1	19.2	52	—
<i>Thalurania nigrofasciata</i> ♂ .....	33	4.3	23.1	57	57
<i>Eriocnemis luciani</i> ♂ .....	27	7.0	36.8	72	73
<i>Phaethornis h. hispidus</i> ♂ .....	26	7.0	25.6	60	60.7
<i>Leucochloris albicollis</i> ♂ .....	32	6.0	25.6	60	60
<i>Aglaeactis cupripennis</i> ♀ .....	15	7.3	52.6	86	87.7
<i>Amazilia tephrocephala</i> ♂ .....	30	5.2	33.9	58	59
<i>Glaucis hirsuta</i> ♀ .....	21	7.0	23.1	57	57.7
<i>Prasites daphne</i> ♂ .....	31	3.1	13.7	44	48
<i>Coeligena torquata</i> ♂ .....	22	7.8	39.9	75	78.7
<i>Heliomaster furcifer</i> ♂ .....	29	5.3	22.3	56	56
<i>Patagona gigas</i> ♂ .....	—	20.0	120	130	132.7
<i>Heliothrix aurita auriculata</i> ♂ .....	19	5.9	30.0	65	65.3
<i>Stephanoxis loddigesi</i> ♂ .....	25	4.0	19.2	52	51.3
<i>Discosura longicauda</i> ♂ .....	40	3.7	14.4	45	—
<i>Agastus superbus</i> ♂ .....	28	3.8	20.7	54	—
<i>Schistes albogularis</i> ♂ .....	30	3.5	18.5	51	—
<i>Campylopterus obscurus aequatorialis</i> ♀ .....	—	7.6	36.8	72	—
<i>Chlorestes n. notatus</i> ♂ .....	28	3.8	17.0	49	—
<i>Thalurania f. baeri</i> ♂ .....	30	4.4	20.7	54	—
<i>Amazilia fimbriata nigricauda</i> .....	25	3.8	20.7	54	—
<i>Thalurania watertoni</i> ♂ .....	32	4.8	20.7	54	—
<i>Anisoterus pretrei</i> ♂ .....	22	5.6	27.3	62	—
<i>Pigmornis nattereri</i> .....	30	3.1	13.1	43	—
<i>ruber ruber</i> ♀ .....	48	2.3	7.74	33	—
<i>idaliae</i> ♀ .....	38	2.4	8.70	35	—
<i>Popelairia langsdorffi langsdorffi</i> ♂ .....	60	3.2	9.22	36	—
<i>Thalurania f. furcata</i> ♂ .....	30	4.2	21.5	55	—
<i>Eupetomena m. simoni</i> .....	20	7.0	36.8	72	—
<i>Amazilia milleri</i> ♂ .....	32	4.1	17.8	50	—

TABLE 10.—DATA ON HUMMINGBIRDS AND OTHER BIRDS  
FROM VARIOUS AUTHORS

The wing-beat rates given here for hummingbirds are believed to have higher precision than those determined by Ruschi and Greenewalt using the portable monocular stroboscope. They were determined either from high-speed moving pictures or with stroboscopic methods of higher precision.

	Wing- beat rate <i>sec-1</i>	Weight of bird <i>gm.</i>	Wing length <i>mm.</i>	Method
M = High-speed moving pictures S = Stroboscopic				
HUMMINGBIRDS: (from Crawford H. Greenewalt, unpublished)				
<i>Calliphlox amethystina</i> ♂ .....	78	—	33 <sup>1</sup>	S
<i>Archilochus colubris</i> ♂ .....	70	—	38.5	M
♀ .....	52	—	44.5	M
<i>Melanotrochilus fuscus</i> .....	25	—	80	S
<i>Amazilia cyanura</i> .....	41.5	—	53	M
<i>Campylopterus hemileucurus</i> .....	27	—	74	M
<i>Microchera albocoronata</i> ♂ .....	52	—	40.5	M
♀ .....	48	—	40.5	M
HUMMINGBIRDS: (from E. Stresemann and K. Zimmer, Ornithologische Monatsberichte, vol. 5 (1932))				
<i>Eupetomena macroura</i> .....	22	6.0	78 <sup>a</sup>	S
<i>Chlorestes caeruleus</i> .....	31.5	3.2	50	S
<i>Chrysolampis elatus</i> .....	32.5	3.5	57	S
<i>Phaëtopernis rufus</i> .....	50.5	2.0	36	S
HUMMINGBIRDS: (from M. Stolpe and K. Zimmer, Journ. Ornithologie, vol. 87, pp. 136-155 (1939))				
<i>Chlorostilbon aureoventris</i> .....	37.5	—	50 <sup>a</sup>	M
<i>Melanotrochilus fuscus</i> .....	28.5	—	80	M
OTHER BIRDS: (from Crawford H. Greenewalt, unpublished)				
<i>Parus carolinensis</i> .....	27	—	65 <sup>4</sup>	M
<i>Sitta carolinensis</i> .....	21	—	92	M
<i>Parus bicolor</i> .....	24	—	82	M
<i>Dendrocopos pubescens</i> .....	18	—	97	M
<i>Mimus polyglottos</i> .....	14	—	112	M
<i>Carpodacus p. purpureus</i> .....	20	—	83	M
Common crow .....	3	—	320	Visual
OTHER BIRDS: (from H. Oehme, Journ. Ornithologie, vol. 100, pp. 363-396 (1959))				
<i>Hirundo rustica</i> .....	6	—	150 <sup>5</sup>	M
<i>Passer domesticus</i> .....	13	—	110	M
<i>Phoenicurus phoenicurus</i> .....	15	—	120	M
<i>Apus apus</i> .....	10	—	170	M
"Haustaub" .....	6	—	310	?
"Nebel krähe" .....	4	—	410	?

Wing length from wing tip to first articulated joint: <sup>1</sup> Ridgway. <sup>2</sup> Authors. <sup>3</sup> Ruschi.  
<sup>4</sup> The American Museum of Natural History (Lanyon). <sup>5</sup> Author.

	Wing span <i>cm.</i>	Wing area <i>cm.</i> <sup>2</sup>
<i>Apus apus</i> .....	38.8	111.2
<i>Hirundo rustica</i> .....	32.9	123.6
<i>Phoenicurus ochruros</i> .....	25.3	106.4
<i>Parus major</i> .....	24.0	99.4
<i>Passer domesticus</i> .....	24.8	103.0
“ <i>montanus</i> .....	22.1	81.6



TABLE 11.—DATA FROM FRANK A. HARTMAN, AUK,  
VOL. 71, NO. 4, PP. 467-469 (1954)  
Cardiac and pectoral muscles of trochilids

	Body weight gm.	Weight of heart % of body weight	Weight of pectoral musculature % of body weight	Wing length* mm.
<i>Glaucis hirsuta affinis</i> ♀ .....	6.13	2.27	27.6	56.5
♂ .....	6.95	—	—	58.6
<i>Phaethornis guy coruscus</i> ♂ .....	5.78	2.40	28.6	61.5
" <i>superciliosus cassinii</i> ♀ .....	6.15	2.19	—	—
" <i>longuemareus saturatus</i> ♀ .....	2.64	2.42	—	37.9
<i>Phaeochroa curvieri</i> ♀ .....	7.95	—	—	68.6
♂ .....	9.30	1.74	—	72.2
<i>Campylopterus hemileucurus</i> ♂ .....	11.92	1.95	33.7	73.9
<i>Florisuga mellivora</i> ♀ .....	6.96	1.83	—	65.2
<i>Colibri thalassinus cabanidis</i> ♀ .....	4.8	—	—	61.0
♂ .....	5.28	1.95	—	66.9
<i>Anthracothonax nigricollis nigricollis</i> ♀ .....	7.33	2.27	—	65.2
♂ .....	6.86	—	—	66.9
<i>Chlorostilbon canivetii assimilis</i> ♀ .....	3.13	1.88	26.5	44.1
♂ .....	3.03	—	—	45.6
<i>Damophila julie panamensis</i> ♀ .....	3.03	2.02	—	42.6
♂ .....	3.35	—	—	43.4
<i>Amazilia amabilis costaricensis</i> ♀ .....	3.85	2.23	—	—
♂ .....	4.78	—	—	—
" <i>decora</i> ♂ .....	4.74	2.30	—	54.0
" <i>edward niveoventer</i> ♀ .....	4.43	2.28	28.5	51.0
♂ .....	4.97	—	—	53.8
" <i>edward</i> ♀ .....	4.15	—	—	52.2
" <i>tzacatl tzacatl</i> ♀ .....	4.72	2.12	26.6	54.9
♂ .....	5.40	—	—	58.3
<i>Eupherusa exima egregia</i> ♂ .....	4.35	2.34	—	60.1
<i>Elvira chionura</i> ♀ .....	2.83	2.25	—	46.8
♂ .....	2.93	—	—	50.3
<i>Chalybura buffonii micans</i> ♀ .....	5.6	—	—	62.0
<i>Lampornis castaneiventris</i> ♀ .....	5.26	2.16	22.5	64.3
<i>Heliodoxa jacula henryi</i> ♀ .....	7.39	1.98	27.9	66.2
<i>Eugenes fulgens spectabilis</i> ♂ .....	5.7	2.16	—	73.5
<i>Heliothrix barroti</i> ♀ .....	5.7	—	—	66.6
<i>Archilochus colubris</i> ♀ .....	3.36	2.31	—	44.5
♂ .....	3.2	—	—	38.5
<i>Selasphorus scintilla</i> ♀ .....	2.23	2.40	24.7	35.7
♂ .....	2.33	—	—	32.7

\* The wing-length measurements are averages taken from Ridgway, "Birds of North and Middle America."

Unpublished data from Frank A. Hartman (Letter to C. H. Greenewalt,  
March 17, 1960)

	Pectoral muscle as % of body weight		Ratio Large/Small
	Large	Small	
<i>Anthracothonax nigricollis</i> .....	21.5	8.6	2.50
<i>Damophila julie</i> .....	16.0	10.5	1.52
<i>Selasphorus scintilla</i> .....	18.2	9.9	1.84
<i>Florisuga mellivora</i> .....	20	10	2.00



TABLE 12.—DATA FROM D. B. O. SAVILLE, AUK, VOL. 67, P. 502 (1950)

	Pectoral muscle as % of body weight		Ratio Large/Small
	Large	Small	
<i>Archilochus colubris</i> .....	20.5	9.2	2.22

TABLE 13.—DATA FROM R. MEINERTZHAGEN, IBIS,  
VOL. 97, NO. 1, PP. 111–114 (1955)

Wing-beat rates—large birds

Wing lengths supplied by Charles Vaurie,  
The American Museum of Natural History

	Wing-beat rate <i>sec-1</i>	Wing length <i>mm.</i>
Raven .....	3.5	455
Carion crow .....	3.6	325
Fantailed raven .....	3.5	371
Rook .....	2.3	315
Jackdaw .....	3.9	237
Jungle crow .....	3.3	377
Magpie .....	3.0	204
Starling .....	5.1	128
Blackbird .....	5.6	125
Cuckoo .....	4.8	222
Short-eared owl .....	2.6	312
Peregrine falcon .....	4.3	309
Barbary falcon .....	4.9	283
Merlin .....	4.9	199
Kestrel .....	3.5	245
Hen harrier .....	3.2	342
Montagu's harrier .....	3.1	360
Black kite .....	2.8	490
Osprey .....	2.4	472
Egyptian vulture .....	2.7	495
Heron .....	2.5	450
Great white egret .....	2.1	437
Flamingo .....	2.4	400
Mute swan .....	2.7	591
Shell duck .....	3.0	375
Mallard .....	5.0	274
Gadwall .....	5.0	271
Wigeon .....	5.1	262
Shoveler .....	5.0	242
Common scoter .....	5.0	235
Velvet scoter .....	4.3	281
Eider duck .....	4.8	289
Merganser .....	4.6	289
Gannet .....	3.0	493
Cormorant .....	3.9	350
Shag .....	4.8	270

TABLE 13.—*concluded*

	Wing-beat rate sec-1	Wing length mm.
Great crested grebe .....	6.3	187
Great northern diver .....	4.2	360
Fulmar .....	3.6	321
Manx shearwater .....	5.1	234
Wood pigeon .....	4.0	245
Rock pigeon .....	4.3	222
Ringed plover .....	5.3	134
Golden plover .....	4.0	190
Lapwing .....	2.3	226
Turnstone .....	4.0	152
Red shank .....	4.2	155
Ruff .....	4.1	192
Oystercatcher .....	4.1	257
Curlew .....	4.0	292
Snipe .....	5.8	133
Greater black-backed gull .....	2.7	497
Lesser black-backed gull .....	2.8	422
Herring gull .....	2.8	438
Common gull .....	3.0	355
Black-headed gull .....	2.8	307
Kittiwake .....	3.3	312
Sandwich tern .....	2.4	308
Puffin .....	5.7	160
Guillemot .....	4.5	200
Black guillemot .....	8.0	163
Coot .....	5.8	212
Pheasant .....	9.0	247
Capercaillie .....	4.6	393

TABLE 14.—DATA FROM EARL L. POOLE, AUK,  
VOL. 55, PP. 511-517 (1938)

## Weights and wing area of 143 species of North American birds

Poole's table is arranged in order of ascending weights and I have retained this format, although it might have been better to group the birds in accordance with families and genera.

The wing areas are for both wings.

Poole did not give wing-length measurements. These have been taken principally from Ridgway's "Birds of North and Middle America" and Forbush's "Birds of Massachusetts and other New England States." The measurements for *Sthenelides olor* and *Columba l. livia* were taken from Witherby's "Handbook of British Birds."

Ridgway's measurements were made with dividers, one point resting against the anterior side of the bend of the wing, the other point touching the extremity of the longest primary. The value given in the table is the average either as reported by Ridgway or obtained by averaging the values given for the extremes.

TABLE 14.—*continued*

Forbush's measurements were made of the folded wing. Here again the value given in the table is the average of the two extremes. It is evident from the good correlation in the charts that Ridgway and Forbush were both measuring the same dimension within a very small error.

In the table that follows, wing-length measurements from Forbush are marked \*; the two from Witherby, \*\*; all others are from Ridgway.

	Weight gm.	Wing area cm. <sup>2</sup>	Wing length cm.
<i>Regulus s. satrapa</i> .....	5.75	51	5.84
<i>Corthylio c. calendula</i> ♂ .....	6.73	58.25	5.89
<i>Setophaga ruticilla</i> ♂ .....	8	62.5	6.35
<i>Certhia familiaris americana</i> ♂ .....	8	66.5	6.55
<i>Dendroica magnolia</i> ♂ .....	9.20	69	6.01
“ <i>v. vierns</i> ♂ .....	9.20	58.5	6.38
“ <i>c. caerulescens</i> ♂ .....	9.25	67	6.52
<i>Nannus h. hiemalis</i> ♂ .....	9.4	41	4.76
<i>Geothlypis trichas brachidactyla</i> ♂ .....	9.5	58.53	5.51
<i>Mniotilta varia</i> ♂ .....	10.5	71	6.86
<i>Troglodytes a. aëdon</i> ♂ .....	11	48.40	5.07
<i>Dendroica pensylvanica</i> ♂ .....	11.1	60.5	6.33
<i>Compsothlypis americana pusilla</i> ♂ .....	11.85	56	6.06
<i>Spizella p. pusilla</i> ♂ .....	12.1	62	6.45
<i>Penthestes a. atricapillus</i> ♂ .....	12.5	76	6.6
<i>Passerina cyanea</i> ♂ .....	13	82	6.78
<i>Spizella p. passerina</i> ♂ .....	13.5	91	6.91
<i>Spinus t. tristis</i> ♂ .....	14	83	7.26
<i>Seiurus n. noveboracensis</i> ♂ .....	14.5	86	7.67
<i>Dendroica coronata</i> ♂ .....	15.5	91	7.41
<i>Stelgidopteryx ruficollis serripennis</i> ♂ .....	15.75	107	11.1
<i>Vireo a. solitarius</i> ♂ .....	16.75	88	7.46
<i>Hirundo erythrogaster</i> ♂ .....	17	118.5	11.8
<i>Melospiza georgiana</i> ♂ .....	17	73	6.25
<i>Chaetura pelagica</i> ♂ .....	17.3	104	12.9
<i>Melospiza l. lincolni</i> ♂ .....	17.8	72.5	6.30
<i>Spizella a. arborea</i> ♂ .....	18	90	7.60
<i>Ammodramus savannarum australia</i> ♂ .....	18.5	89	6.10
<i>Anthus spinoletta rubescens</i> ♀ .....	19	109	8.19
<i>Sayornis phoebe</i> ♀ .....	20	134.5	8.33
<i>Iridoprocne bicolor</i> ♂ .....	20.1	125	11.74
<i>Junco h. hyemalis</i> ♂ .....	21.5	99	7.93
<i>Melospiza m. melodia</i> ♂ .....	22	86.5	6.73
<i>Baeolophus bicolor</i> ♂ .....	22.5	117.8	7.98
<i>Icterus spurius</i> ♂ .....	23	100.5	7.82
<i>Passer d. domesticus</i> ♂ .....	24.5	92.5	7.60
<i>Carpodacus p. purpureus</i> ♂ .....	24.5	104	8.33
<i>Dryobates pubescens medianus</i> ♂ .....	24.8	136	9.41
<i>Bombicilla cedrorum</i> ♂ .....	25	130	9.38
<i>Oceanodroma l. leucorhoa</i> .....	26.5	251	15.9*
<i>Zonotrichia albicollis</i> ♂ .....	26.5	108	7.47
<i>Poocetes g. gramineus</i> ♂ .....	27	108	8.10
<i>Hylocichla guttata faxonii</i> ♂ .....	29.5	116	9.44
“ <i>f. fuscescens</i> ♂ .....	32.3	147	10.23
<i>Sialia s. sialis</i> ♂ .....	32.7	148	10.01
<i>Hylocichla minima aliciae</i> ♂ .....	34	150	10.40

TABLE 14.—continued

	Weight gm.	Wing area cm. <sup>2</sup>	Wing length cm.
<i>Piranga flava hepatica</i> ♂	35.8	153	10.26
<i>Dumetella carolinensis</i> ♂	39	150	9.12
<i>Hedymeles ludovicianus</i> ♂	40	166.5	10.14
<i>Passerella i. iliaca</i> ♂	40.5	116	8.92
<i>Pipilo e. erythrophthalmus</i> ♂	41.7	145	8.92
<i>Progne s. subis</i> ♂	43	185.5	14.63
<i>Hedymeles m. melanocephalus</i> ♂	44.7	200	9.98
<i>Tringa s. solitaria</i> ♂	47	192	12.65
<i>Actitis macularia</i> ♂	47.5	146	10.05
<i>Pinicola enucleator leucura</i> ♂	50	189	11.41
<i>Molothrus a. ater</i> ♂	50.5	179	11.05
<i>Coccyzus a. americanus</i> ♂	61	266	14.36
<i>Rallus l. limicola</i> ♂	65	221	10.59
<i>Agelaius p. phoeniceus</i> ♂	70	245	12.09
<i>Balanosphyra f. formicivora</i> ♂	74.5	306	14.11
<i>Porzana carolina</i> ♂	75	176	10.70
<i>Chordeiles m. minor</i> ♂	75.25	349.5	19.80
<i>Turdus m. migratorius</i> ♂	82	244	13.43
<i>Sturnus v. vulgaris</i> ♂	84	190.3	12.90
<i>Oxyechus v. vociferus</i> ♂	85	275	16.02
<i>Centurus carolinus</i> ♂	87	262	13.10
<i>Cyanocitta c. cristata</i> ♂	89	236	13.15
<i>Alle alle</i> ♂	96	146	11.58
<i>Accipiter v. velox</i> ♂	97.5	439	17.11
<i>Colaptes auratus luteus</i> ♂	100	324	15.63
<i>Pisobia melanotos</i> ♂	101	199	13.98
<i>Cyanocephalus cyanocephalus</i> ♂	108	390	15.40
<i>Cryptoglaux a. acadica</i> ♂	108	420	13.63
<i>Capella delicata</i> ♂	112	250	12.71
<i>Quiscalus q. quiscula</i> ♂	122.3	324	14.38
<i>Zenaidura macroura carolinensis</i> ♂	130	357.5	14.72
<i>Valco s. sparverius</i> ♀	137	372	19.5
<i>Sturnella m. magna</i> ♂	145	265	12.24
<i>Megascyle a. alcyon</i> ♂	155	376	15.63
<i>Totanus melanoleucus</i> ♂	170	412	18.78
<i>Accipiter v. velox</i> ♀	171	607	20.03
<i>Falco c. columbarius</i> ♂	173	410	18.89
<i>Otus asio naevius</i> ♂	178	523	16.02
<i>Philohela minor</i> ♂	198.5	354.66	12.35
<i>Colinus v. virginianus</i> ♂	198.64	216.8	11.15
<i>Rallus e. elegans</i> ♂	227	536	16.34
<i>Butorides v. virescens</i>	230	660	18.1*
<i>Asio wilsonianus</i> ♂	230	1,182	29.20
<i>Otus asio naevius</i> ♀	254	476	16.60
<i>Corvus ossifragus</i> ♀	273.5	912.5	27.15
<i>Asio wilsonianus</i> ♀	288	1,198	29.39
<i>Corvus ossifragus</i> ♂	309	1,072	27.80
<i>Columba l. livia</i>	314	567	21.93**
<i>Nettion carolinense</i>	321	374	17.5*
<i>Querquedula discors</i>	332	370	18.4*
<i>Gallinula chloropus cachinnans</i> ♂	332	479.5	17.45
<i>Podilymbus p. podiceps</i>	343.5	291	12.4*
<i>Colymbus auritus</i>	369.5	350	14.5*
<i>Buteo p. platypterus</i> ♂	376	1,012	26.28
<i>Charitonetta albeola</i>	377	412	16.4*
<i>Circus hudsonius</i> ♂	414	1,382	33.96
<i>Accipiter cooperi</i> ♂	428.5	898	23.10

TABLE 14.—concluded

	Weight gm.	Wing area cm. <sup>2</sup>	Wing length cm.
<i>Fulica a. americana</i> ♂ .....	435	596	19.03
<i>Florida c. caerulea</i> .....	449	1,246.5	26.0*
<i>Tyto alba partincola</i> ♂ .....	505	1,683	32.86
<i>Sirix v. varia</i> ♂ .....	510	1,830	33.28
<i>Bonasa u. umbellus</i> ♂ .....	516.5	527	18.36
<i>Corvus b. brachyrhynchos</i> ♂ .....	552.5	1,344	32.10
<i>Spatula clypeata</i> .....	570	570	24.1*
<i>Aix sponsa</i> ♂ & ♀ .....	589	660	22.7*
<i>Circus hudsonius</i> ♀ .....	615	1,696	36.75
<i>Botaurus lentiginosus</i> .....	625	1,258	29.2*
<i>Erismatura jamaicensis rubida</i> .....	635	394	14.7*
<i>Falco peregrinus anatum</i> ♂ .....	712	1,146	31.42
<i>Chaulelasmus streperus</i> .....	723	718	26.2*
<i>Nyroca collaris</i> .....	757.31	460	19.7*
“ <i>affinis</i> ♀ .....	763	472	20.0*
<i>Nycticorax nycticorax hoactli</i> .....	804	1,773	30.4*
<i>Buteo l. lineatus</i> ♂ .....	804	1,656	32.08
<i>Astur a. atricapillus</i> ♂ .....	848.6	1,480	32.52
<i>Larus argentatus smithsonianus</i> ♂ .....	850	2,006	41.0
<i>Buteo b. borealis</i> ♂ .....	875	1,878	36.96
<i>Casmerodius albus egretta</i> .....	899	2,528	38.1*
<i>Dafila acuta tsitsihos</i> .....	970	761	26.2*
<i>Branta bernicla hrota</i> .....	1,024	1,264	33.6*
<i>Clangula hyemalis</i> ♂ .....	1,038	550.48	22.1*
<i>Buteo lagopus s. johannis</i> ♂ .....	1,110	2,592	40.74
<i>Anas rubripes tristis</i> ♀ .....	1,142	1,007	26.2*
<i>Falco peregrinus anatum</i> ♀ .....	1,222.5	1,342	35.63
<i>Anas p. platyrhynchos</i> ♀ .....	1,233.5	952	27.9*
<i>Phasianus colchicus torquatus</i> ♂ .....	1,304	917	23.41
<i>Buteo b. borealis</i> ♀ .....	1,307	2,294	38.88
<i>Astur a. atricapillus</i> ♀ .....	1,370	2,004	33.36
<i>Nyctea nyctea</i> ♂ .....	1,404	2,576	40.81
<i>Anas p. platyrhynchos</i> ♂ .....	1,408	1,029	27.9*
<i>Bubo v. virginianus</i> ♀ .....	1,446.5	2,534	36.63
“ <i>virginianus pacificus</i> ♂ .....	1,480	2,426	33.65
<i>Pandion haliaetus carolinensis</i> ♂ .....	1,797.5	3,211	47.74
<i>Ardea h. herodias</i> .....	1,905	4,436	48.1*
<i>Cathartes aura septentrionalis</i> ♂ .....	2,409	4,356	53.59
<i>Gavia i. immer</i> ♀ & ♂ .....	2,425	1,358	36.0*
<i>Meleagris gallopavo silvestris</i> ♀ .....	3,897	3,752	41.43
<i>Aquila chrsaetos canadensis</i> ♀ .....	4,664	6,520	63.32
<i>Branta c. canadensis</i> .....	5,662	2,820	46.4*
<i>Cygnus columbianus</i> .....	5,943	4,156	55.0*
<i>Sthenelides olor</i> ♀ .....	11,602	6,808	55.25**
HUMMINGBIRDS:			
<i>Archilochus alexandri</i> ♂ .....	2.55	12.75	4.27
“ <i>colubris</i> ♂ .....	2.98	12.40	3.85



TABLE 15.—DATA FROM A. MAGNAN, ANN. SCI. NATURELLE,  
SER. 10, VOL. 5, PP. 125-334 (1922)

## Les caractéristiques des oiseaux

Magnan has divided his birds into groups in accordance with their mode of flight. His short titles are difficult to translate, and I have left them in the original French. The basis for his classification is given on pages 165-171 of the original paper, together with the French common names of the species.

In addition to the data presented in the following tables, Magnan has measured many other characteristics, such as, for example, the length of body, length of tail, weight of wing skeleton, weight of heart, etc. I have given here those measurements which seemed particularly pertinent to flight.

The one measurement which presents difficulties is that of wing spread. Magnan says "The measurement is a matter of individual judgment; it is essential that all species be measured by the same hand, the wings must be stretched in precisely the same manner. The point is important, not if the wing spreads differ by a factor of 2, but if the differences are small."

All measurements appear to have been made with the greatest care. Captive birds were used, and those which appeared to be in bad health were discarded. Nowhere else in the literature is there such an abundance of data. For anyone interested in dimensional relationships the entire paper is well worth careful study.

	Total weight gm.	Wing area cm. <sup>2</sup>	Wing weight gm.	Wing spread cm.	Wing length cm.	Pectoral muscles weight, gm. Large    Small	
Rapaces diurnes voiliers							
<i>Gyps fulvus</i> .....	7,269	10,540	1,599	255.7	69.8	958	61.8
<i>Gypaëtus barbatus grandis</i> .....	5,385	7,431	1,279	252.4	71.7	715	46.8
<i>Catharista atrata</i> .....	1,702	3,012	327	140.8	50.2	299	15.3
<i>Aquila chrysaetos</i> .....	3,712	5,382	813	212.1	68.2	476	25.6
<i>Hieraëus fasciatus</i> .....	2,060	3,172	408	155.2	56.0	223	14.6
<i>Helotarsus ecaudatus</i> .....	2,095	3,582	406	153.6	51.2	270	12.4
<i>Geranoatus melanoleucus</i> .....	2,123	3,550	402	145.3	51.5	194	10.8
<i>Circus gallicus</i> .....	1,655	4,121	400	181.0	53.3	226	10.9
<i>Buteo bueto</i> .....	1,027	2,691	181	132.2	40.4	113.5	8.94
<i>Pernis apivorus</i> .....	615	1,894	109	119.9	45.1	79.8	3.88
<i>Pandion haliaetus</i> .....	1,105	2,921	310	157.2	49.6	149	8.84
<i>Circus aeruginosus</i> .....	680	2,264	141	134.5	41.3	84.2	3.74
“ <i>cyaneus</i> ♀ .....	471.5	1,759	101	116.7	37.4	73.8	3.25
“    “    ♂ .....	331	1,406	70.1	104.4	33.9	53.8	2.28
“ <i>pygargus</i> .....	236.5	1,296	61.5	110.1	35.9	36.0	1.63
“ <i>macrurus</i> .....	386	1,413	75.1	110.7	35.7	48.0	1.93
<i>Milvus milvus</i> .....	927	2,902	218	162.8	50.7	151	7.88
Palmipèdes voiliers							
<i>Diomedea exulans</i> .....	8,502	6,206	1,377	340.8	67.4	1,036	59.5
<i>Fregata aquila</i> .....	1,620	3,240	326	201.9	61.0	186	9.7
<i>Sula bassana</i> .....	2,690	2,450	390	183.6	48.7	323	20.7
<i>Puffinus kuhli</i> .....	572	1,280	98.0	121.1	34.9	67.3	4.2
<i>Hydrobates pelagicus</i> .....	17.40	100	2.61	33.2	12.4	2.44	0.16
<i>Larus marinus</i> .....	1,915	2,719	394	172.6	50.9	228	23.0

TABLE 15.—*continued*

	Total weight gm.	Wing area cm. <sup>2</sup>	Wing weight gm.	Wing spread cm.	Wing length cm.	Pectoral muscles weight, gm. Large      Small	
Échassiers ramo-planeurs							
<i>Ardea cinerea</i> .....	1,408	3,590	329	172.6	43.7	217	16.2
<i>Egretta alba</i> .....	1,178	2,827	225	144.7	43.3	161	14.1
<i>Botaurus stellaris</i> .....	1,198	2,696	171	132.9	35.1	167	17.2
<i>Nycticorax nycticorax</i> .....	512	1,577	78.0	104.8	27.2	69.1	7.5
<i>Platalea leucorodia</i> .....	1,565	2,488	282	137.0	37.2	266	24.4
<i>Ciconia ciconia</i> .....	3,438	4,951	670	197.8	55.9	537	48.2
<i>Megalornis grus</i> .....	4,175	5,553	810	211.0	56.4	550	65.6
<i>Leptopilius crumeniferis</i> .....	7,030	8,225	1,516	281.7	78.6	1,202	103.6
<i>Vanellus vanellus</i> .....	211	668	38.6	75.0	22.6	44.0	4.1
Rapaces nocturnes ramo-planeurs							
<i>Bubo bubo</i> .....	1,720	3,715	366	164.1	43.1	246	13.1
<i>Asio otus</i> .....	247	1,082	49.9	94.1	31.5	27.3	1.73
“ <i>flammeus</i> .....	390	1,396	75.0	107.5	32.9	46.4	2.57
<i>Otus scops</i> .....	49.75	405	11.3	52.3	15.1	4.70	0.27
<i>Tyto alba</i> .....	279	1,163	54.5	97.3	28.1	33.2	2.15
<i>Strix aluco</i> .....	418	1,304	76.1	95.0	22.4	39.5	2.30
<i>Athene noctua</i> .....	161.5	459	25.3	58.9	19.6	18.0	1.19
Rapaces diurnes ramo-planeurs							
<i>Accipiter gentilis</i> .....	708	1,317	113	100.7	30.3	105.5	3.75
“ <i>nisus</i> ♀ .....	221	822	46.9	75.0	23.6	45.1	2.34
“ “ ♂ .....	136	530	28.2	62.2	19.0	22.8	1.24
<i>Polyborus tharus</i> .....	1,209	2,321	224	135.4	41.6	148.5	9.55
<i>Falco tinnunculus</i> ♀ .....	245	708	42.4	73.8	23.2	28.3	1.64
“ “ ♂ .....	172	703	30.5	75.1	25.6	21.2	1.55
“ <i>peregrinus</i> .....	813	1,285	153	106.4	34.5	148.6	6.58
“ <i>subbuteo</i> .....	165	558	32.1	75.7	25.2	30.0	1.44
“ <i>columbarius regulus</i> .....	145	438	23.8	60.4	24.7	27.9	1.35
Corvidés ramo-planeurs							
<i>Corvus corone</i> .....	470	1,058	74.7	89.4	29.5	60.9	4.89
“ <i>cornix</i> .....	633	1,317	96.0	97.9	31.8	86.0	6.14
<i>Trypanocorax frugilegus</i> .....	470	1,387	80.0	97.2	31.9	69.2	5.08
<i>Coloeus monedula spermologus</i> .....	253	665	37.0	70.8	23.4	33.5	2.73
<i>Pyrhocorax pyrrhocorax</i> .....	390	948	58.5	67.2	26.3	52.7	3.90
<i>Graculus graculus</i> .....	223	997	36.5	78.2	27.9	27.8	2.14
<i>Nucifraga caryocatactes</i> .....	161	515	21.8	59.8	18.5	22.5	2.05
<i>Coracias garrulus</i> .....	128	483	18.9	61.5	19.7	16.0	1.60
<i>Pica pica</i> .....	214	640	31.4	59.2	19.1	26.8	2.18
<i>Garrulus glandarius</i> .....	160	554	20.9	54.3	19.0	18.9	1.93
<i>Upupa epops</i> .....	91	366	12.3	47.7	15.7	14.3	1.09
<i>Xanthoura yncas</i> .....	71.3	316	9.27	37.3	14.1	7.80	0.87
Passereaux ramo-planeurs							
<i>Cuculus canorus</i> .....	104	419	20.3	58.3	19.8	19.5	1.64
<i>Caprimulgus europaeus</i> .....	92	398	16.1	56.9	19.4	16.6	1.85
<i>Apus apus</i> .....	36.2	165	4.99	42.0	17.5	6.75	0.90
<i>Chelidon rustica</i> .....	18.35	135	2.71	33.0	11.9	3.40	0.33
<i>Hirundo urbica</i> .....	14.35	92.0	1.80	29.2	10.0	1.90	0.17
<i>Riparia rupestris</i> .....	15.50	119	2.25	31.4	11.2	2.52	0.165
Palmipèdes ramo-planeurs							
<i>Phalacro corax carbo</i> .....	2,115	1,967	265	171	42.4	262	26.5
<i>Puffinus puffinus</i> .....	342	575	45.5	81.1	23.8	42.6	4.10
<i>Larus argentatus</i> .....	1,189	2,105	226	143	46.6	141	12.1
“ <i>canus</i> .....	367	1,149	71.0	108	34.4	47.0	3.60

TABLE 15.—*continued*

	Total weight gm.	Wing area cm. <sup>2</sup>	Wing weight gm.	Wing spread cm.	Wing length cm.	Pectoral muscles weight, gm. Large Small	
Palmipèdes ramo-planeurs, <i>continued</i>							
<i>Rissa tridactyla</i> .....	488	967	71.7	105	32.3	65.0	6.30
<i>Larus ridibundus</i> .....	261	853	42.5	97.1	30.7	33.3	3.00
<i>Sterna hirundo</i> .....	118	563	22.0	82.9	28.4	19.0	1.90
Passereaux rameurs a vol soutenu							
<i>Muscicapa striata</i> .....	14.35	119	1.80	26.7	8.99	2.10	0.20
<i>Ficedula hypoleuca</i> .....	12.50	91.0	1.38	24.4	7.89	1.95	0.20
<i>Alauda arvensis</i> .....	28.30	163	3.65	31.7	9.45	6.05	0.55
<i>Anthus pratensis</i> .....	18	96.8	2.11	25.9	7.86	3.91	0.35
“ <i>trivialis</i> .....	20.70	125	2.54	28.6	9.06	3.97	0.38
<i>Motacilla alba</i> .....	22	132	3.05	28.3	8.97	4.55	0.38
“ <i>flava</i> .....	16.50	101	2.00	25.0	7.64	3.40	0.26
“ <i>cinerea</i> .....	16	92.0	1.94	25.2	8.06	3.70	0.29
<i>Lanius excubitor</i> .....	50.50	210	5.80	35.5	11.1	7.22	0.77
“ <i>senator</i> .....	26.10	144	3.05	31.4	11.0	3.80	0.39
“ <i>collurio</i> .....	30.95	182	2.82	28.6	8.79	3.20	0.30
<i>Luscinia megarhyncha</i> .....	17.1	100	1.70	25.5	8.24	2.35	0.29
<i>Erythacus rubecula</i> .....	17.75	88.0	1.65	22.7	6.78	2.14	0.25
<i>Phoenicurus phoenicurus</i> .....	13	91.0	1.45	25.6	7.99	2.26	0.22
“ <i>ochrurus</i> .....							
“ <i>gibraltariensis</i> .....	16.95	122.4	2.10	27.0	8.73	2.50	0.25
<i>Pratincola rubetra</i> .....	13.05	98.8	1.55	23.5	7.77	2.04	0.20
“ <i>cubicola</i> .....	11.45	76.8	1.20	21.6	6.54	1.68	0.17
<i>Phylloscopus bonellii</i> .....	7.65	63.0	0.80	19.1	5.71	1.20	0.14
“ <i>rufus</i> .....	5.25	48.2	0.60	17.4	5.39	0.65	0.10
<i>Oriolus oriolus</i> .....	72	274	9.91	47.0	15.39	14.7	1.22
<i>Monticola solitarius</i> .....	62.8	236	6.59	38.6	12.32	8.40	0.82
“ <i>saxatilis</i> .....	47.5	160	4.38	35.5	11.23	7.25	0.70
<i>Turdus merula</i> .....	91.5	260	8.99	40.6	12.62	14.6	1.70
“ <i>naumanni</i> .....	76.2	225	7.15	37.7	11.87	11.3	1.35
“ <i>viscivorus</i> .....	106	307	11.25	44.0	14.20	22.5	1.80
“ <i>pilaris</i> .....	98	225	9.90	42.9	13.83	22.8	1.84
“ <i>musicus</i> .....	70.3	191	6.64	36.7	11.14	14.0	1.40
“ <i>iliacus</i> .....	56	180	5.70	37.1	11.48	10.9	1.00
“ <i>torquatus</i> .....	96.5	222	8.85	42.7	13.30	15.7	1.59
<i>Sturnus vulgaris</i> .....	79.5	192	7.96	39.1	12.47	15.0	1.54
<i>Loxia curvirostra</i> .....	47.6	167	5.82	31.9	10.16	10.3	1.02
<i>Coccothraustes coccothraustes</i> .....	42	148	4.65	32.0	9.73	8.18	0.87
<i>Pyrrhula p. europaea</i> .....	21.4	94.8	2.35	25.5	8.05	3.20	0.40
<i>Serinus canarius serinus</i> .....	8.35	73.1	1.17	22.1	7.10	1.83	0.17
<i>Choris chloris</i> .....	23.70	100	2.75	27.0	8.62	5.75	0.47
<i>Fringilla caelebs</i> .....	21.15	102	2.75	28.5	8.85	4.95	0.40
“ <i>montifrigilla</i> .....	25.1	123	2.90	28.1	9.08	4.10	0.40
<i>Passer domestica</i> .....	30	101	2.90	25.2	7.46	4.85	0.49
“ <i>montana</i> .....	15.2	76.0	1.58	21.8	7.18	2.55	0.33
<i>Petronia petronia</i> .....	25	100	2.30	28.4	9.06	4.90	0.49
<i>Carduelis carduelis</i> .....	16.65	92.1	2.10	24.8	7.91	3.42	0.35
<i>Spinus spinus</i> .....	11.80	68.0	1.24	21.4	6.83	2.42	0.17
<i>Acanthus cannabina</i> .....	15.80	96.1	1.85	24.8	8.03	3.60	0.36
<i>Spinus citrinella</i> .....	11.95	73.9	1.45	24.5	7.31	2.40	0.25
<i>Emberiza citrinella</i> .....	25	130	3.36	28.1	9.06	5.00	0.55
“ <i>cirlus</i> .....	23.1	104	2.60	24.8	7.40	4.70	0.40
“ <i>hortulana</i> .....	33	122	2.45	27.3	8.66	4.20	0.48
“ <i>cia</i> .....	21.40	108	1.78	25.8	7.77	3.95	0.32
“ <i>schoeniclus</i> .....	20	114	1.65	25.5	7.60	4.00	0.30
<i>Regulus regulus</i> .....	3.80	32.2	0.40	14.3	5.00	0.45	0.05

TABLE 15.—*continued*

	Total weight gm.	Wing area cm. <sup>2</sup>	Wing weight gm.	Wing spread cm.	Wing length cm.	Pectoral weight, gm. Large	muscles Small
Passereaux rameurs a vol peu soutenu							
<i>Cyanecula suesica cyanecula</i> .....	14.30	78.9	1.64	21.4	6.31	1.75	0.26
<i>Sylvia atricapilla</i> .....	16.25	88.9	1.75	23.8	7.60	1.75	0.23
“ <i>jimplex</i> .....	15.8	74.9	1.52	23.6	7.53	1.58	0.22
“ <i>communis</i> .....	18.65	87.1	1.69	22.5	7.16	2.20	0.25
<i>Prunella modularis</i> .....	18	80.1	1.55	22.0	6.55	2.40	0.24
<i>Hypolais icterina</i> .....	10.65	80.0	0.88	20.5	6.60	1.18	0.14
<i>Acrocephalus cirpaceus</i> .....	12.80	67.2	1.00	20.3	6.78	1.52	0.18
“ <i>schoenobaenus</i> .....	10.40	52.9	0.98	19.2	6.11	1.22	0.14
<i>Parus major</i> .....	21.45	102	1.60	23.3	7.50	2.75	0.25
“ <i>caeruleus</i> .....	11	66.0	0.98	21.4	6.67	1.77	0.18
“ <i>cristatus mitratus</i> .....	10.20	72.9	1.26	20.2	6.29	1.42	0.15
“ <i>palustris longirostris</i> .....	10.90	64.1	1.14	20.0	6.21	1.75	0.17
“ <i>communis</i> .....	11.75	71.9	1.20	20.9	6.82	1.70	0.17
<i>Aegithalus caudatus</i> .....	8	58.0	0.73	18.6	6.00	1.25	0.12
<i>Gecinys viridis</i> .....	156	457	20.5	51.7	16.15	25.4	1.95
<i>Dryobates major pinetorum</i> .....	73	238	9.75	42.2	12.95	13.0	1.14
“ <i>minor hortorum</i> .....	15.50	103	1.90	26.9	8.48	2.50	0.25
<i>Jynx torquilla</i> .....	37.30	116	3.58	29.4	8.69	6.95	0.48
<i>Certhia brachydactyla</i> .....	8.50	66.0	0.92	20.0	6.12	1.25	0.13
<i>Sitta europaea coesia</i> .....	21.10	132.7	2.55	27.4	8.57	3.20	0.30
<i>Trichodroma muraria</i> .....	15	174	2.25	30.1	9.86	2.30	0.17
<i>Troglodytes troglodytes</i> .....	10.1	41.4	0.75	16.9	4.76	1.15	0.15
Passereaux vibrateurs							
<i>Eupherusa eximia</i> .....	2.85	15.4	0.18	13.0	5.10	0.86	0.12
Échassiers rameurs terrestres							
<i>Otis tarda</i> .....	8,950	5,728	1,298	208	51.9	1,790	224
“ <i>tetrax</i> .....	830	1,038	120	86.5	22.6	182	22.5
<i>Burhinus oedicephalus</i> .....	522	757	71.0	83.7	23.4	81.3	9.20
<i>Charadrius apricarius</i> .....	178	356	20.3	58.5	17.4	41.2	6.04
“ <i>morinellus</i> .....	90	247	9.9	46.6	14.8	20.1	2.75
<i>Crex crex</i> .....	155	318	16.1	47.8	14.0	24.3	3.35
<i>Scolopax rusticola</i> .....	322	596	37.5	66.5	20.6	82.0	17.8
Échassiers rameurs riverains							
<i>Numenius arquatus</i> .....	768	1,175	108	104.4	30.2	145	18.0
<i>Haematopus ostralegus</i> .....	438	622	64.0	80.5	25.8	65.6	8.68
<i>Charadrius hiaticula</i> .....	62.2	188	5.90	40.8	13.1	10.7	1.30
<i>Squatarola squatarola</i> .....	216	413	23.8	65.4	20.4	40.7	5.20
<i>Gallinago gallinago</i> .....	95.5	244	9.29	44.8	12.8	25.3	5.20
<i>Lymnocyrtus gallinula</i> .....	57	178	6.40	39.3	10.8	11.3	2.24
<i>Canutus canutus</i> .....	88	269	11.2	50.3	15.6	18.7	2.46
<i>Eriolia alpina</i> .....	44	126	3.65	36.0	10.9	8.45	1.10
<i>Arenaria interpres</i> .....	107.8	213	9.80	47.6	14.8	22.4	3.04
<i>Calidris leucophaea</i> .....	41.9	160	4.20	35.4	11.5	8.60	1.52
<i>Machetes pugnax</i> .....	180	457	22.5	63.2	19.2	41.3	5.18
<i>Tringa nebularius</i> .....	156	406	18.5	60.8	18.8	33.8	4.64
“ <i>erythropus</i> .....	133	326	15.5	54.1	16.3	28.6	4.39
“ <i>totanus</i> .....	133	366	14.2	51.6	14.8	26.2	3.79
“ <i>ocrophus</i> .....	72.7	248	8.35	47.2	14.6	18.2	3.00
“ <i>hypoleucus</i> .....	48.5	148	4.25	35.7	11.3	8.10	1.52
<i>Limosa lapponica</i> .....	197	520	27.6	73.3	22.1	40.4	7.80
“ <i>limosa</i> .....	228	527	30.3	69.0	20.8	51.7	7.00
<i>Recurvirostra avocetta</i> .....	295	684	41.6	77.2	22.0	49.4	3.98



TABLE 15.—*continued*

	Total weight gm.	Wing area cm. <sup>2</sup>	Wing weight gm.	Wing spread cm.	Wing length cm.	Pectoral muscles weight, gm. Large Small	
Colombins rameurs							
<i>Columba palumbus</i> .....	495	797	70.0	75.1	24.5	118	18.5
“ <i>aenas</i> .....	306	532	44.3	75.3	20.9	73.9	12.3
<i>Turtur turtur</i> .....	178	376	24.5	52.9	17.5	39.4	7.30
Gallinacés rameurs							
<i>Tetrao urogallus</i> ♂ .....	3,361	1,412	339	131.8	36.0	607	208
“ “ ♀ .....	1,890	1,219	206	91.5	33.6	413	116
<i>Lyrurus tetrix</i> ♂ .....	1,030	968	105	83.8	23.2	238	74.0
“ “ ♀ .....	940	846	96.9	76.4	21.6	144	57.0
<i>Tetrao medius</i> .....	1,193	978	130	87.0	25.5	270	75.4
<i>Lagopus mutus</i> .....	462.5	486	42.0	60.3	18.6	78.7	21.1
“ <i>lagopus</i> .....	620	626	57.3	68.2	21.3	124	37.2
“ <i>scoticus</i> .....	624	593	56.0	70.9	21.4	122	36.5
<i>Tetrastes bonasia</i> .....	278	386	21.5	52.9	16.3	73.0	24.7
<i>Caccabis rufa</i> .....	490	519	42.7	54.4	16.6	91.2	32.2
<i>Caccabis saxatilis</i> .....	606.5	473	48.2	55.0	16.1	92.6	31.2
<i>Perdix perdix</i> .....	387	433	30.4	52.5	15.3	83.6	28.6
<i>Coturnix coturnix</i> .....	83.2	171	7.60	35.8	10.5	14.75	4.13
<i>Colinus pectoralis</i> .....	131.5	196	9.89	33.1	9.66	26.1	9.86
<i>Rhynchotus rufescens</i> .....	821.7	657	61.6	67.4	21.5	159	37.0
Palmipèdes nageurs rameurs							
<i>Cygnus cygnus</i> .....	5,925	3,377	978	230	56.1	884	70.1
<i>Anser fabalis</i> .....	3,110	2,675	425	162	46.7	555	59.7
“ <i>anser</i> .....	3,065	2,697	491	163	46.5	570	59.8
“ <i>albifrons</i> .....	1,715	1,835	294	141	40.7	309	39.3
<i>Branta bernicla</i> .....	1,273	1,388	165	119	33.6	209	22.9
“ <i>leucopsis</i> .....	1,150	1,150	150	108	35.6	192	20.8
<i>Anas platyrhynchos</i> .....	1,105	928	117	90.0	25.9	215	32.7
<i>Spatula clypeata</i> .....	633	614	66.0	79.8	23.2	116	15.2
<i>Dafila acuta</i> .....	955	840	98.0	91.6	25.6	186	20.0
<i>Mareca penelope</i> .....	830	664	83.6	85.5	25.4	146	17.7
<i>Querquedula crecca</i> .....	293	349	31.0	57.8	17.9	57.7	7.33
“ <i>querquedula</i> .....	327	399	36.2	65.4	19.3	63.4	8.90
<i>Clangula clangula</i> .....	622	516	57.0	70.0	19.6	106	14.5
<i>Nyroca nyroca</i> .....	512	512	50.0	68.0	18.4	86.8	10.25
“ <i>fuligula</i> .....	741	474	55.9	70.6	20.8	123	13.55
“ <i>ferina</i> .....	842	615	80.0	77.4	21.7	166	16.4
“ <i>marila</i> .....	675	621	98.6	81.6	21.9	176	16.3
<i>Oidemia nigra</i> .....	870	679	88.0	85.0	22.9	102	12.2
“ <i>fusca</i> .....	1,578	1,010	160	96.7	25.6	218	26.8
Palmipèdes plongeurs rameurs							
<i>Mergus serrator</i> .....	818	589	77.7	88.6	24.4	142	14.7
“ <i>mergamser</i> .....	1,470	853	167	95.5	26.2	213	22.0
“ <i>albellus</i> .....	495	431	41.0	62.5	17.4	86.5	9.37
<i>Colymbus cristatus</i> .....	790	561	72.0	78.6	17.6	92.0	8.90
“ <i>griseigena</i> .....	480	542	43.2	72.0	16.4	57.2	5.28
“ <i>ruficollis</i> .....	180	236	10.9	44.0	10.2	14.65	1.95
<i>Gavia septentrionalis</i> .....	957	890	102	104	26.6	58.0	5.55
“ <i>arctica</i> .....	1,495	1,196	168	120	30.9	147	10.45
<i>Alca torda</i> .....	780	382	48.0	68.1	19.3	97.0	28.9
<i>Uria troille</i> .....	1,010	424	61.9	70.2	20.1	148	48.0
<i>Fratercula arctica</i> .....	272	345	23.7	56.4	16.2	30.4	9.50
<i>Alle alle</i> .....	91.2	167	7.75	38.7	12.6	12.8	3.65



TABLE 15.—*concluded*

	Total weight <i>gm.</i>	Wing area <i>cm.<sup>2</sup></i>	Wing weight <i>gm.</i>	Wing spread <i>cm.</i>	Wing length <i>cm.</i>	Pectoral muscles weight, <i>gm.</i>	
						Large	Small
Échassiers plongeurs rameurs							
<i>Fulica atra</i> .....	578	618	40.5	72.5	20.0	57.3	7.30
<i>Gallinula chloropus</i> .....	265	368	21.0	55.9	12.8	33.0	4.70
<i>Porzana porzana</i> .....	69	228	6.44	39.4	11.5	9.15	1.45
<i>Rallus aquaticus</i> .....	128	261	9.50	41.3	11.6	11.4	2.14
Passereaux plongeurs rameurs							
<i>Alcedo ispida</i> .....	36.4	108	3.75	28.8	8.29	6.02	0.76

## LITERATURE CITED

GREENEWALT, CRAWFORD H.

1960. The wings of insects and birds as mechanical oscillators. *Proc. Amer. Philos. Soc.*, vol. 104, No. 6, pp. 605-611, 4 figs.

HARTMAN, FRANK A.

1954. Cardiac and pectoral muscles of trochilids. *Auk*, vol. 71, No. 4, pp. 467-469.

HOCKING, B.

1953. The intrinsic range and speed of flight of insects. *Trans. Roy. Ent. Soc. London*, vol. 104, pt. 8, pp. 223-345, 6 pls., 29 figs.

MAGNAN, A.

1922. Les caractéristiques des oiseaux suivant le mode de vol. *Ann. Sci. Nat.*, ser. 10, vol. 5, pp. 125-334, 37 figs., 14 pls.

1934. *Le vol des insectes*. Hermann et Cie, Paris.

MAGNAN, A., and PERRILLIAT-BOTONET, Ch.

1932. Sur le poids relatif des muscles moteurs des ailes chez les insectes. *Compt. Rend. Acad. Sci.*, vol. 195, pp. 559-561.

MEINERTZHAGEN, R.

1955. The speed and altitude of bird flight (with notes on other animals). *Ibis*, vol. 97, No. 1, pp. 81-117.

MÜLLENHOFF, KARL.

1885. Die Grösse der Flugflächen. *Pflueger's Arch. Ges. Physiol.*, vol. 35, pp. 407-453, 4 figs.

OEHME, HANS.

1959. Untersuchungen über Flug und Flügelbau von Kleinvögeln. *Journ. Orn.*, vol. 100, No. 4, pp. 363-396, 30 figs.

POOLE, EARL L.

1938. Weights and wing area of 143 species of North American birds. *Auk*, vol. 55, pp. 511-517.

REED, S. C. ; WILLIAMS, C. M. ; and CHADWICK, L. E.

1942. Frequency of wing-beat as a character for separating species races of geographic varieties of *Drosophila*. *Genetics*, vol. 27, No. 3, pp. 349-361.

SAVILE, D. B. O.

1950. The flight mechanism of swifts and hummingbirds. *Auk*, vol. 67, pp. 499-504.

SOTAVALTA, OLAVI.

1947. The flight-tone (wing-stroke frequency) of insects. *Acta Entomologica Fennica*, pt. 4, 117 pp., 18 illus.
1952. The essential factor regulating the wing-stroke of insects in wing mutilation and loading experiments and in experiments at sub-atmospheric pressure. *Ann. Zool. Soc. "Vanamo,"* vol. 15, No. 2, 66 pp., 12 figs.
1954. The effect of wing inertia on the wing-stroke frequency of moths, dragonflies and cockroach. *Ann. Ent. Fennica*, vol. 20, No. 3, pp. 93-101.

STRESEMANN, E., and ZIMMER, K.

1932. Ueber die Frequenz des Flügelschlages beim Schwirrflug der Kolibris. *Orn. Monatsb., Jahrg.* 40, No. 5, pp. 129-133.

NOTE: After completion of the present manuscript I have noted Frank A. Hartman's "Locomotor Mechanisms of Birds" (*Smithsonian Misc. Coll.*, vol. 143, No. 1). This paper contains many data on dimensional relationships for birds. A cursory inspection of the tables indicates general agreement with the relationships presented here. It is unfortunate that I was unable to include Hartman's excellent and abundant data in the present compilation.—C. H. G.





SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 144, NUMBER 3  
(END OF VOLUME)

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Charles D. and Mary Vaux Walcott  
Research Fund

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# REVISION OF THE CASSIDULOID ECHINOIDS

(WITH 44 PLATES)

By

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(PUBLICATION 4500)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
JUNE 26, 1962



PORT CITY PRESS, INC.  
BALTIMORE, MD., U. S. A.

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(WITH 44 PLATES)

### INTRODUCTION

During preparation of the chapter on the Cassiduloida for the "Treatise on Invertebrate Paleontology," it became obvious that this group could not be properly understood without considerable research. Mortensen (1948) made a great contribution to knowledge of the cassiduloids, but unfortunately he saw few of the fossil species and was misled by the many inaccurate descriptions and illustrations by previous authors. Only by reexamining the primary types or topotype specimens of the type species, could the systematic outline of the cassiduloids be determined. This task has taken nearly five years, requiring two trips to European museums and extensive borrowing of specimens. Specimens of the type species of nearly all the genera have been studied, including the 71 genera that have been considered as synonyms. The results agree with the findings of Durham (1955, p. 74), that although the illustrations by previous workers appear to be carefully drawn, many are very inaccurate. Furthermore, most authors have not included drawings of the phyllodes, a feature which has proved to be of the utmost importance to the classification of this group.

The order Cassiduloida, as restricted herein, includes all those "irregular" echinoids having petals, phyllodes, and bourrelets (the floscelle). These structures are illustrated in the included figure of a typical cassiduloid (text fig. 1). The phyllodes are formed by the crowding of pores in the ambulacra near the mouth (peristome). The bourrelets are caused by a swelling of the interambulacral plates at the peristome. There are 67 genera and approximately 800 species.

They first appeared in the Lower Jurassic, increased in number of species throughout the Mesozoic, and reached their zenith in the Eocene. Very few species are living today.

In the course of this study, some interesting evolutionary trends have been discovered, suggesting many lineages within the cassiduloids. Perhaps the most striking of these trends is the abrupt reduction from two pores to one pore in each ambulacral plate beyond the petals, and the introduction of buccal pores. These changes occurred in almost all cassiduloids in the Cenomanian. Likewise an abrupt change in the structure of the apical system occurred at the end of the Cretaceous, with most pre-Maestrichtian species having a tetrabasal system and all Tertiary species having a monobasal system.

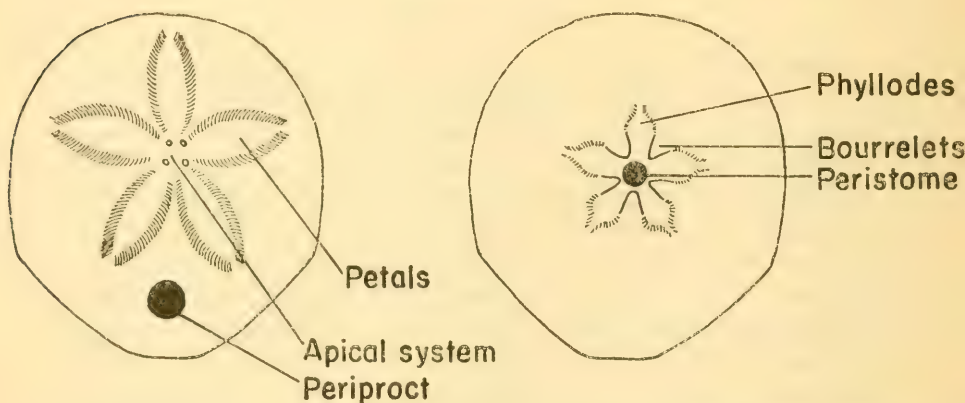


FIG. 1.—An adapical and adoral view of a typical cassiduloid echinoid. The phyllodes are formed by the crowding of ambulacral pores near the peristome. The floscelle is the starlike structure formed by the phyllodes and the bourrelets.

#### ACKNOWLEDGMENTS

The National Science Foundation generously provided two grants which made possible two trips to Europe to collect and to study in museums in Paris, Basel, Geneva, Brussels, Liège, London, and Cambridge. I am greatly indebted to Richard V. Melville, who accompanied me on a fossil-hunting trip in France and who was of great assistance. General Collignon, Prof. A. Jeannet, Count Lecointre, and Roger Brun very kindly accompanied us on part of this trip and guided us to many echinoid localities. Max Meijer and Dr. G. Ubaghs took me to several excellent echinoid localities in Belgium.

Here in the U. S. National Museum, I am indebted to Dr. Richard S. Boardman, who has critically read the manuscript and made many



excellent recommendations. Dr. Richard F. Grant made many helpful suggestions throughout this study, and he and Thomas R. Waller edited the section on evolution. Dr. Ellis Yochelson assisted in many nomenclatural problems, and I thank Dr. Norman F. Sohl for his information on the Upper Cretaceous stratigraphy of the eastern United States and for his large collections of specimens of *Hardouinia*. I am particularly indebted to Dr. G. Arthur Cooper for his support of this study. The charts and the figure illustrating the morphology of a cassiduloid were made by Lawrence B. Isham, scientific illustrator, Department of Geology, U. S. National Museum, and many of the photographs were taken by Jack Scott. My wife, Mary, encouraged me throughout this work.

This study would not have been possible without the assistance of the many museum curators who lent specimens or made their collections available for study. Their generosity exceeded my highest expectations, and because of their help I was able to see many specimens that had never been adequately described or figured, and some that were presumed lost. Listed below are the names of these curators and their institutions.

#### BRAZIL

Departemento Nacional da Producao Mineral, Rio de Janeiro: Dr. Lamego, Dr. Santos.

#### EGYPT

Geological Museum, Cairo: Dr. M. Saber Mansour.

#### FRANCE

Bordeaux: Université de Bordeaux, Faculté des Sciences: Dr. M. Vigneuas.  
Paris: Muséum National d'Histoire Naturelle: Dr. Jean Roman and Dr. J. Sornay. École National Supérieure des Mines: Dr. Paul Fischer, and Madame Letia. Université de Paris, Sorbonne: Dr. D. Laurentiaux.  
Strasbourg: Université de Strasbourg, Laboratoire de Geologie et de Paleontologie: M. Wolf.

#### FRENCH WEST AFRICA

Dakar: Université de Dakar: Prof. F. V. L. Tessier.

#### GERMANY

Berlin: Geologisch—Paläontologisches Institut und Museum der Humboldt—Universität zu Berlin: Dr. W. Gross.  
Bonn: Geologisch-palaeontologisches Institut und Museum der Rhein. Friedrich Wilhelms-Universität: Dr. Hans Mensink.  
Munich: Bayerische Staatssammlung für Paläontologie und historische Geologie: Dr. Hans K. Zobelein.

#### GREAT BRITAIN

Cambridge: Sedgwick Museum: A. G. Brighton.  
Exeter: Royal Albert Memorial Museum: Dr. R. Churchill Blackie.  
Glasgow: Hunterian Museum: Dr. Ethel D. Currie.  
London: British Museum (Natural History): Dr. Leslie Bairstow.

## HUNGARY

Budapest: Hungarian Geological Institute: Dr. Erzsebet Szorenyi, Dr. Jozsef Fulop.

## INDIA

Calcutta: Geological Survey of India: Dr. V. R. Khedker.

## POLAND

Warsaw: Polska Akademia Nauk: Dr. Gertruda Biernat.

## PORTUGAL

Lisbon: Serviços Geológicos de Portugal.

## SICILY

Palermo: Istituto di Geologia: Dr. Giuliano Ruggieri.

## SWITZERLAND

Basel: Naturhistorisches Museum: Dr. E. Gasche, Dr. Hans Kugler.

Genève: Muséum D'Histoire Naturelle: Dr. E. Lanterno.

Zurich: Geologisches Institut: Dr. R. Trumphy.

## U.S.A.

Austin, Tex.: University of Texas: Dr. Keith Young.

Baltimore, Md.: Johns Hopkins University: Dr. David Raup.

Berkeley, Calif.: University of California: Dr. J. Wyatt Durham.

Cambridge, Mass.: Harvard University, Museum of Comparative Zoology:  
Dr. Harry B. Whittington, Dr. E. Deichmann.

Chicago, Ill.: Chicago Natural History Museum: Dr. Eugene S. Richardson, Jr.

Ithaca, N. Y.: Paleontological Research Institution: Dr. Katherine Palmer.

New York, N. Y.: American Museum of Natural History: Dr. Norman D. Newell.

Philadelphia, Pa.: Academy of Natural Sciences: Dr. Horace G. Richards.

San Francisco, Calif.: California Academy of Sciences: Dr. Leo G. Hertlein.

## U.S.S.R.

Leningrad: Geological Museum of the Academy of Sciences of the U.S.S.R.:  
Dr. Z. Krjachkova.

Moscow: The Palaeontological Institute of the Academy of Sciences of  
the U.S.S.R.: Dr. J. Orlov.

## EVOLUTION

## AMBULACRAL PORES

There is a striking example of parallel evolution in the ambulacra of the cassiduloids. In the species occurring before the Cenomanian, there are pore pairs in all the ambulacral plates, but in all those occurring after the Senonian, there are only single pores in the ambulacral plates beyond the petals. This change is graphically shown in chart 1, in which all the genera below the bold line have double pores beyond the petals, and all those above this line have a single pore. That such a change was forthcoming is indicated by the reduction in size in one of the pores of a pore pair in many pre-Cenomanian and

QU

TERTIARY

JASIDA

CRETACEOUS

PYGUOSTOMA

PETALOBRISSUS

JURASSIC

lloida.









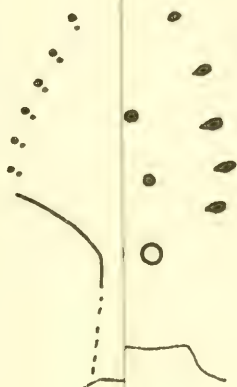
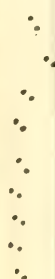
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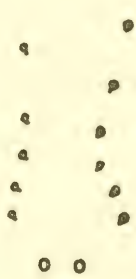
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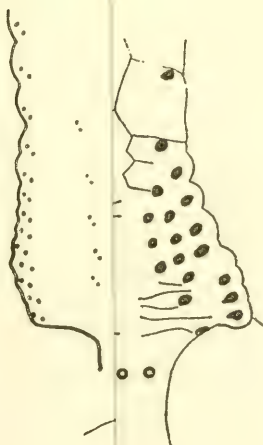
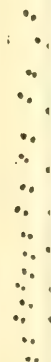
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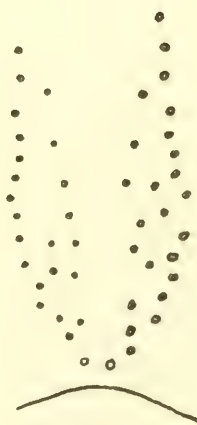
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X



W



Y

S - BUCCAL PORES

Each species are recorded  
*orbignyana* (Cotte  
 er; P, *Hypopygura*  
*everaladensis* (Ma



# EVOLUTION OF THE NUCLEOLITID TYPE PHYLLODE IN THE CASSIDULOIDA

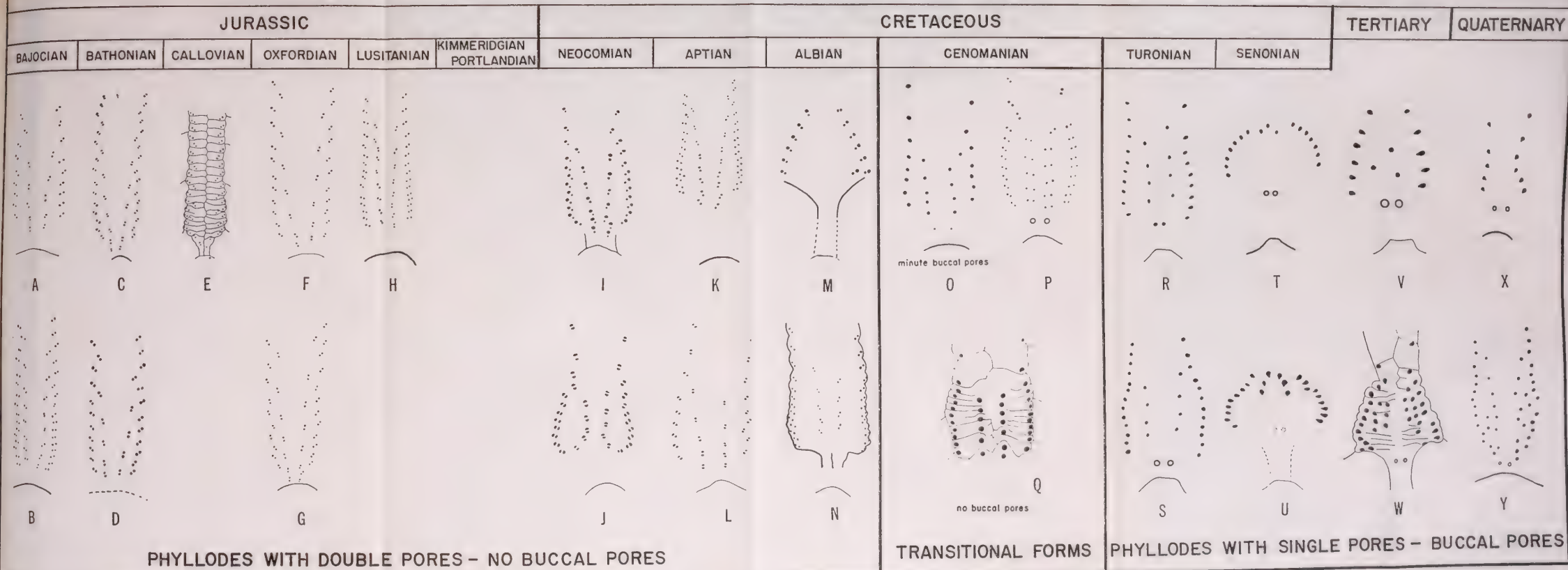


CHART 2.—The evolution of the nucleolitid type phyllode in the Cassiduloidea. The locality data and location of the specimen of each species are recorded in the systematic portion of the text. A, *Nucleolites forsteri* (Cotteau); B, *N. hui* (Agassiz); C, *N. amplius* (Agassiz); D, *N. burgundiae* (Cotteau); E, *Botheopneustes lamberti* Fourtau; F, *N. sentatus* Lamarck; G, *N. aculeatus* (Agassiz); H, *Pseudosirella obliqua* (Cotteau); I, *Pyrochordus obliquus* (Agassiz); J, *Pyrochordus pindus* (Cotteau); K, *Phyllobranchia corallina* (Desor); L, *Phyllobranchia excentricus* (Pictet and Renevier); M, *Ochetes morrisii* (Forbes); N, *Pyrochordus columbianus* (Cooke); O, *Gentia systemus* Kier; P, *Hyponeris aeneus* (Lambert); R, *Phyllobranchia lefevrei* (Fourtau); S, *Parapneustes tenuis* (Folger); T, *Harlanina enigmata* (Stephenson); U, *Pyrochordus excentricus* Clark; V, *Phyllobranchia quaternaria* (Cotteau); W, *Rhynchonella pindus* (Mansueti); X, *Cassidulus carolinensis* (Lamark); Y, *Rhynchonella pindus* (Bell).





Cenomanian species, such as the Neocomian *Pygorhynchus obovatus* Agassiz (chart 2, fig. I), and *Phyllobrissus gresslyi* (Agassiz) (text fig. 61), the Albian *Ochetes morrisii* (Forbes) (chart 2, fig. M) and the Cenomanian *Catopygus carinatus* (Goldfuss) (text fig. 55) and *Catopygus bagesii* (d'Orbigny) (text fig. 59).

Although this study is concerned primarily with the cassiduloids, it is of interest to note that a very similar reduction in pores occurs in the spatangoids. I have not studied as many species of spatangoids, but most of those examined fall into a consistent pattern very similar to that in the cassiduloids. Over a brief period of time, all the spatangoids of the many diverse families undergo reduction of extra-petaloid pores from two to one. This change differs from the corresponding change in the cassiduloids by occurring later, at the end of the Cretaceous. Furthermore, no buccal pores are introduced.

It is surprising that this parallelism in reduction from pore pair to single pore within the cassiduloids and the spatangoids has never been observed before. Mortensen (1948, p. 178) noted that several species had been reported as having single pores in the ambulacral plates but considered this fact of no significance. One reason that this trend was not discovered earlier is that many of the figures showing the phyllodes have been erroneous. Cotteau's artist always showed double pores in the phyllodes whether they were double or single. Of the hundreds of species of irregular echinoids figured in "Paleontologie Francaise, Terrain Tertiaire," all are shown as having double pores in the ambulacral plates beyond the petals, although double pores do not occur in any of them. Hawkins (1911) in his study of the phyllodes did not study any post-Cenomanian species, or he certainly would have discovered this trend.

The reason for this change from two pores to one pore in the cassiduloids and spatangoids seems to be reasonably clear. Most of the Paleozoic and early Mesozoic regular echinoids used their tube-feet for breathing as well as for feeding and locomotion. To fulfill the respiratory function, it was necessary that the tube-feet bifurcate in order to maintain two separate currents of water, one with oxygen and one without. According to MacBride (1906, p. 517), in *Echinus* "the tube-foot is connected by a double canal with the ampulla, the object of which is to assist in respiration. The cells lining it are ciliated, and produce a current up one side of the tube-foot and down the other, and the double canal leading to the ampulla separates these two currents and prevents them interfering with one another." Therefore, each tube-foot had a pair of pores linking it to the exterior. There

were no petals in these regular echinoids, and the whole ambulacrum was used partially for respiration. Most of the adoral portion of the test was not in contact with the sea floor, but was elevated by spines and by the spherical shape of the test.

With the development of the irregular echinoid, the living habits changed radically. Prior to this change, most echinoids probably lived on the top of the sea floor, but in the Jurassic the irregular echinoids began to burrow shallowly into the substrate. In order to burrow, many changes in the morphology of the echinoid were necessary. Many regular echinoids were aided in respiration by large gills situated around the mouth. These gills could not function when the echinoid was partially buried, and their function was transferred adaptively with the development of the petals. The tube-feet in the adapical ambulacra altered greatly in shape, with a great lateral expansion of the outer branch of each tube-foot, greatly increasing its oxygen-absorbing area. Furthermore, the test became greatly flattened, with the reduction in size of the spines, its lower surface came in contact with the sea floor. The adoral tube-feet no longer could be used very effectively for respiration, and they were adapted for food gathering. The phyllodes resulted from the crowding of these tube-feet around the peristome. The tube-feet between the phyllodes and the petals assumed a sensory function, as in the living spatangoids (Nichols, 1959, p. 399). Simultaneously with these developments, the jaws disappeared, and the eating habits of the echinoids altered greatly. Echinoids with jaws ate larger food particles, but without jaws the particle size was greatly reduced, necessitating ingestion of many more particles. Presumably the great increase in the number of tube-feet around the mouth resulted from the need to have some means of conveying a great number of food particles to the mouth. Probably these tube-feet later became more specialized for this function, and fewer were needed, explaining the decrease in number of pores in the phyllodes of many of the Cretaceous cassiduloids. According to Hyman (1955, p. 434), in the living echinoids the tube-feet of the phyllodes are greatly specialized and are pencillate with the ends of the feet expanded and covered with erect club-shaped projections. Because these tube-feet were not used for respiration, it was not necessary for each foot to have an incurrent and excurrent channel, and for the pores to be paired. Probably the current in a tube-foot not used for respiration is unidirectional at one time, and the partition necessary for a pore pair would obstruct

this current. Furthermore, a double-pored ambulacrum is structurally weaker than one with a series of single pores.

Almost simultaneous with the reduction from two pores to one, another very significant and important feature appears: the first buccal pores, through which extended tube-feet that were presumably sensory in function and aided in the detection of food. In general, species with double pores lack buccal pores, and species with single pores have them. There are few exceptions to this combination, and most of these exceptions occur in species that lived during the transitional period when the first single pores appeared, such as *Hypopygurus gaudryi* Gauthier (chart 2, fig. P), in which there are buccal pores but the ambulacra are all double pored; *Gentilia tafileltensis* ? Lambert (chart 2, fig. Q), with single pores but no buccal pores, and *Gentilia syriensis* Kier (chart 2, fig. O), with minute buccal pores.

#### PHYLLODES

The phyllodes in the cassiduloids can be divided into two types: the nucleolitid and the pygurid. The pygurid type is found in many species of the Galeropygidae and the Clypeidae, and is particularly well exhibited in *Pygurus*. In this genus, there is a remarkably consistent trend in the evolution of the phyllodes, with a broadening of the phyllodes, a reduction in the number of pore pairs, and an increase in the distance between the pores and the edge of the peristome. This trend is illustrated in chart 3. In order to assure objectivity in this study, I have included on this chart a drawing of a phyllode of *all* the well-dated species of *Pygurus* in which this area has been figured.

In the Middle Jurassic species of *Pygurus*, such as *P. (Mepygurus) depressus* Agassiz (chart 3, fig. a) from the Bathonian, the phyllodes are very long, not broadened, and have many pore pairs arranged in three series in each half-ambulacrum. The pore pairs extend almost to the edge of the peristome. Callovian species such as *P. (Mepygurus) marmonti* (Beaudouin) (chart 3, fig. b) and *P. (Mepygurus)* sp. (chart 3, fig. c) from Madagascar have similar phyllodes except for a slight broadening of the phyllode near the peristome. By Lusitanian time, the phyllodes have changed considerably. In *P. (Pygurus) geryvillensis* Peron and Gauthier (chart 3, fig. e) and *P. (Pygurus) blumenbachi* Kock and Dunker (chart 3, fig. d) the phyllodes are greatly broadened, with the pore pairs shifted more laterally to the edge of the ambulacrum with a wide area between the two inner series of each half-ambulacrum. The pore pairs terminate far from the edge of the peristome, and there are fewer pore pairs in the inner



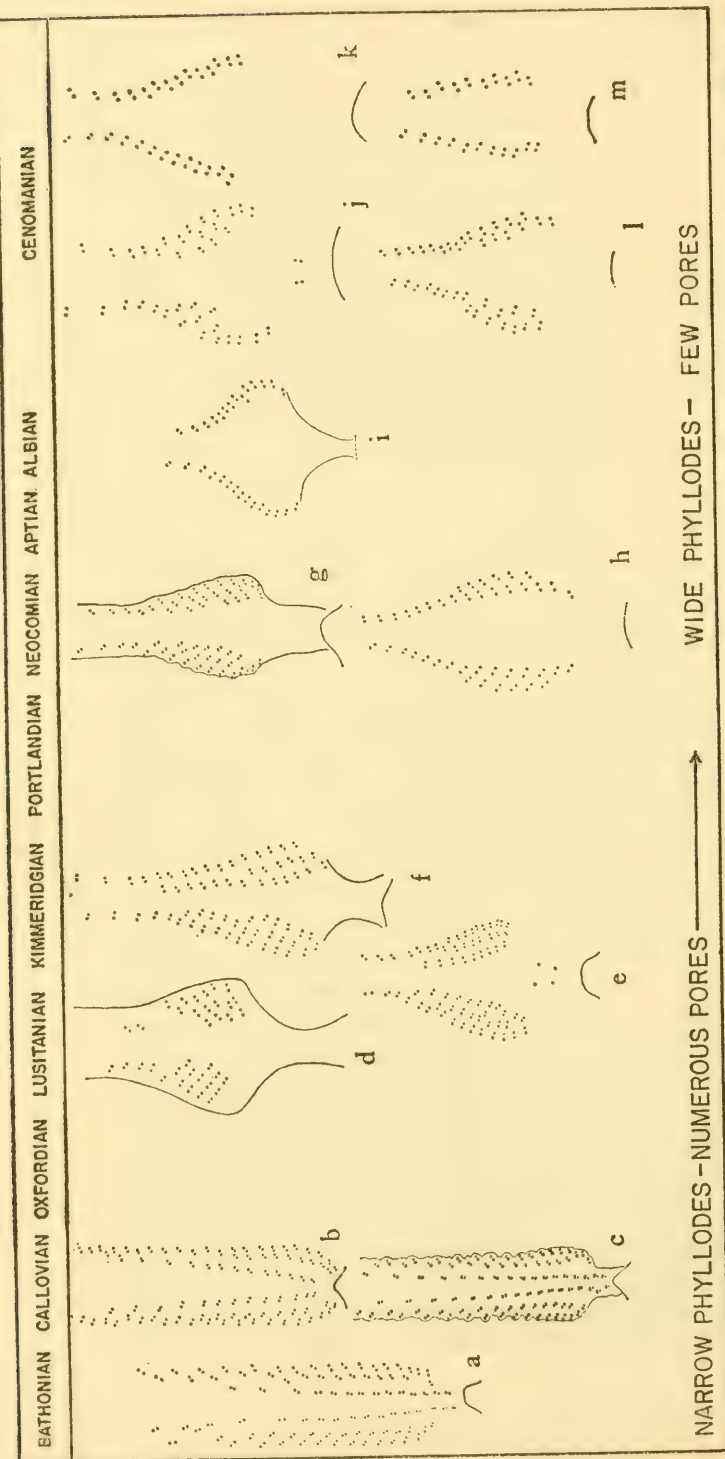


CHART 3.—Evolution of the phylloides in *Pygurus*. a, *Pygurus* (*Mcpygurus*) *depressus* Agassiz, ambulacrum II of specimen in École National Supérieure des Mines, Paris, from Gorze, France; b, *Pygurus* (*Mcpygurus*) *marnontii* (Beaudouin) adapted from Cotteau (1869, Pal. franc. Jur., pl. 32, fig. 5); c, *Pygurus* (*Mcpygurus*) sp., ambulacrum IV of specimen in collection of General Collignon, from the Callovian of Madagascar; d, *Pygurus* (*Pygurus*) *blumenbachii* Kock and Dunker, ambulacrum IV of Cotteau's (1869, Pal. franc. Jur., pl. 38, fig. 3, pl. 39, pl. 40, fig. 1) figured specimen in the École National Supérieure des Mines, Paris, from the Coral Rag, Thury (Yonne), France; e, *Pygurus* (*Pygurus*) *gervillienensis* Peron and Gauthier, ambulacrum I of lectotype in Lambert Collection, at the Sorbonne, Paris, from Dra el Ahmar, Geryville, Algeria; f, *Pygurus* (*Pygurus*) *perreti* Lambert, copied and adapted from Lambert (1905b, pl. 22, fig. 24); g, *Pygurus* (*Pygurus*) *rostratus* (Agassiz), ambulacrum IV of specimen in Museum of Comparative Zoology, Harvard, from Ste. Croix, Switzerland; h, *Pygurus* (*Pygurus*) *montmolini* (Agassiz), copied and adapted from d'Orbigny (1856, pl. 917, fig. 4); i, *Pygurus* (*Pygurus*) *jagweyanus* Cooke, ambulacrum V of paratype of USNM 108698, from 10 km. north of Fonseca, Magdalena, Colombia; j, *Pygurus* (*Pygurophis*) *noctingi* De Loriol, ambulacrum I of holotype in De Loriol's collection in the Muséum d'Histoire Naturelle, Geneva, Switzerland, from Kef Akab, Ouadi Sanin, Lebanon; k, *Pygurus* (*Pygurus*) *lampas* (De la Beche), ambulacrum IV from specimen in École National Supérieure des Mines, Paris, from Le Mans, France; l, m, *Pygurus* (*Pygurus*) *africanus* De Loriol, copied and adapted from De Loriol (1888, pl. 7, figs. 2, 3a).

series. The phyllodes of the Kimmeridgian *P. (Pygurus) perreti* Lambert (chart 3, fig. f) and of the Neocomian species *P. (Pygurus) rostratus* (Agassiz) (chart 3, fig. g) are similar, being broad and having three series of pore pairs in each half-ambulacrum. In the Neocomian *P. (Pygurus) montmollini* (Agassiz) (chart 3, fig. h) the phyllodes have evolved to just two series of pore pairs in each half-ambulacrum. By Albian and Cenomanian time there is only one series as in *P. (Pygurus) jagueyanus* Cooke (chart 3, fig. i), *P. (Pygurus) lampas* (De la Beche) (chart 3, fig. k) and *P. (Pygurus) africanus* De Loriol (chart 3, figs. l, m). It is interesting to note that in one of the phyllodes of one of the specimens of *P. africanus* figured by De Loriol there is a very short inner series. In *P. (Pyguroopsis) noctlingi* De Loriol (chart 3, fig. j) there are two to three series of pore pairs but only for a short distance, with a single series near the peristome.

In the nucleolitid type phyllode, there is not the same evolutionary trend from the Bajocian to the Cenomanian as that found in the pygurid type. As can be seen on chart 2, where the phyllodes of 24 representative species are figured, the Lower Cretaceous phyllodes are very similar to those of the Middle Jurassic (Bajocian). Throughout this period all the species, except for *Ochetes morrisii* (Forbes) (chart 2, fig. M) have two series of pore pairs in each half-ambulacrum. The phyllodes of six species of *Nucleolites* (chart 2, figs. A, B, C, D, F, G) are very similar even though they do not occur at the same time. Even phyllodes of different genera are basically similar as shown in *Bothryopneustes* (chart 2, fig. E), *Pseudosorella* (chart 2, fig. H), *Pygorhynchus* (chart 2, fig. I), *Plagiochasma* (chart 2, fig. L), *Phyllobrissus* (chart 2, fig. K), and *Clypeopygus* (chart 2, J). However, during and after the Cenomanian the number of pores in each plate is reduced from two to one, as described above, and buccal pores appear. In the Turonian, most of the species have moderately widened phyllodes with two series of pores in each half-ambulacrum such as in *Petalobrissus* (chart 2, fig. R) or *Parapygus* (chart 2, fig. S). From this time through the Senonian there is an evolutionary trend in many genera toward a widening of the phyllodes, and a reduction in the number of pores in each inner series, such as in *Hardouinia* (chart 2, fig. T) and *Pygidiolampas* (chart 2, fig. U). This trend in *Hardouinia* is described in detail on page 146. In the Tertiary and Recent genera there is a relationship between the size of the test and the number of pores in the phyllode. Genera with small tests such as *Pliolampas* (chart 2, fig. V) and *Cassidulus* (chart 2,



fig. X) have phyllodes with few pores, whereas species of *Rhyncholampas* (chart 2, fig. W) and *Echinolampas* (chart 2, fig. Y) with large tests, have phyllodes with many pores. It is significant that even the young tests of large species have more pores than tests of the same size of small species.

#### PETALS

There is a most striking evolutionary trend in the relationship between the length of the petals and the position of the margin. This trend is illustrated in chart 4, in which all the important genera are represented. The black area in each top and side view is the area below the petals. In Middle Jurassic and Callovian genera the petals are long and the margin abrupt, so that the area below the petals is very small. By the Oxfordian the petals are still very long, but the test is somewhat higher resulting in more area below the petals, particularly in side view. From this time onward there is a rapid increase in the area below the petals due to a combination of shorter petals and a higher test with steeper sides. As discussed in more detail on p. 21, a cassiduloid probably could not burrow deeper than the lower limit of its petals. Therefore, apparently the reason for this change is that this increase in the area below the petals enabled the echinoid to burrow deeper into the substratum. There are many advantages in being able to burrow. That portion of the test under the sand would be less vulnerable to damage by wave action, and there would be less possibility of the test being tipped over. Furthermore, partially buried echinoids would have more protection from predators, because the test would be less visible and less exposed to the teeth or drill of an adversary. Finally, the ability to burrow would greatly increase the feeding area for the echinoid. When he was confined to the top of the substratum, all his food came from the top surface and the area within the substratum that could be reached by his phyllodal tube-feet. Burrowing increased this area by the volume of the substratum through which the animal was able to burrow.

Besides the above evolutionary trend, there are several other changes in the petals. In the Jurassic species the petals are normally very long, extending to the margin of the test, and either narrow and almost subpetaloid as in *Galeropygus agariciformis* (Wright), or very broad and open with the outer pores greatly elongated and strongly conjugate as in *Clypeus*. The only exception to this generality is *Nucleolites*, in which the petals are shorter and narrower than in *Clypeus*. In the Lower Cretaceous there are fewer species having the broad








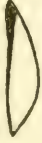
TERTIARY		QUATERNARY	
Miocene	PLIOLAMPAS		
Oligocene Eocene			
Paleocene	EURRHODIA		
Bojocian			
			
			

CHART 4.—Adapical and side view of specimens of type species of principal cassiduloid genera. The area below the petals is shown in black and may represent that part of the test that was buried in life. As can be seen from the chart, in the older species there is less area below the petals.



CHART 4.—Adapical and side view of specimens of type species of principal cassidoid genera. The area below the petals is shown in black and may represent that part of the test that was buried in life. As can be seen from the chart, in the older species there is less area below the petals.

QUATERNARY		TERTIARY		CRETACEOUS		JURASSIC																																													
Pliocene	 CASSIDULUS 	 RHYNCHOLAMPAS 	 ECHINOLAMPAS 	Paleocene	 EURHODIA 	Senonian	 RHYNCHOPYGUS 	 HARPOCINIA 	 GITOLAMPAS 	 PETALOBRISSUS 	Cenomanian	 CAROPYGUS 	Albian				Neocomian	 PYGOURUS (PYGURUS) 	 PHYLLOBRISUS 	 PYGAULUS 	 PLAGIOCASSINA 	Portlandian				Kimmeridgian				Lusitanian				Oxfordian	 NUCLEOLITES 				Callowian	 PYGURUS (MEPYGURUS) 				Bathonian	 HYDOCYPUS 				Bajocian	 CYPEUS 	 GALEROPYGUS 





petals so common in the Jurassic, and a predominance of species with open petals and narrow outer poriferous zones such as in *Pygaulus*, *Catopygus*, *Clypeopygus*, and *Pygorhynchus*. In the Upper Cretaceous there is a tendency toward shorter, closed petals with broader outer poriferous zones, such as in *Petalobrissus*, *Zuffardia*, *Lcfortia*, *Fauraster*, and *Faujasia*. In the Maestrichtian Cassidulidae, the petals are slightly developed and inconspicuous. A new feature is developed in the Tertiary with the introduction of unequal poriferous zones in the same petal. Usually the right poriferous zone in petal III is longer than the left, the posterior zones in petals II and IV longer than the anterior and the anterior longer in petals V and I. This inequality in length is very common in the Tertiary, occurring in almost all the species of *Rhyncholampas*, *Cassidulus*, and *Echino-lampas*. The function of this inequality is not known.

In almost every genus all the ambulacra are petaloid. The only exceptions are *Archiacia*, *Gentilia*, *Claviaster*, and *Pseudopygaulus* in which ambulacrum III is nonpetaloid, or the petal is greatly reduced. Lambert thought that there was no petal III in *Heteronucleus*, *Pseudonucleus*, and *Pseudopygurus*, but I have examined the type specimens of these genera under high magnification and found petal III. There was probably a petal III in the adult of *Sphelatus*, but the type specimen is immature and the petal not developed.

#### APICAL SYSTEM

The apical system undergoes considerable evolution from the Jurassic to the Recent, changing from a tetrabasal system with or without complementary and catenal plates to a monobasal system without any extra plates. In the Jurassic species, the system is tetrabasal, has four genital pores, and may have (text figs. 30-35) many complementary and catenal plates. The number and arrangement of these plates are very variable, even down to the species level. In some specimens of *Clypeus agassizi* (Wright), there are catenal plates joining the apical system to the periproct, but in other specimens there are none. Likewise, in *Nucleolites scutatus* Lamarck catenal and complementary plates may or may not be present. Early Cretaceous species still have a tetrabasal apical system and four genital pores, but there are no catenal or complementary plates. In the Late Cretaceous beginning with the Turonian, there are species with only three genital pores. In the Senonian an abrupt change occurs, with many species having monobasal apical systems with only one genital plate, presumably genital 2. This change is very rapid and all inclusive for

there are no tetrabasal systems in adults of any post-Cretaceous species. On chart 1, all those genera having monobasal apical systems are above the bold dashed line, and all those with tetrabasal systems below.

It is not possible to tell whether or not this change to a monobasal system was caused by fusion of the genital plates, resorption, or nondevelopment of genitals 1, 3, 4, 5. There is no trend toward increase in the size of genital plate 2 and no corresponding decrease in the size of the other genitals. In one of the earliest cassiduloids, *Clypeus agassizi* (text fig. 13) genital 2 is just as large, and the other genitals as small as in later species such as *Petalobrissus setifensis* Cotteau from the Senonian. Gordon (1929, p. 310) found in the Recent species *Echinarachnius parma* Lamarck that only one genital plate ever formed, with the other three present only in the form of remnants of larval spicules. Hyman (1955, p. 533) says that "in the Cassidulidae the four genital plates are fused with the madreporite," but she gives no evidence for this statement.

This change from a tetrabasal to a monobasal apical system is remarkable not only because of its parallelism in all the lineages of the cassiduloids that extend into the Tertiary, but also because of the abruptness with which it occurs. The lack of any trend toward a reduction in the size of the other genital plates, and the absence of any specimen with a monobasal apical system before the Senonian, suggests that this change was produced by parallel mutations and parallel selection. It might be suggested that the reason for the change is that a monobasal apical system is structurally stronger because it lacks the sutural area found in a tetrabasal system. However, almost all pre-Senonian cassiduloid specimens have their apical systems preserved intact. It is, therefore, difficult to understand why a tetrabasal apical system would simultaneously become such a lethal character for all cassiduloids. Perhaps the mutations that produced the monobasal system were linked with another feature of greater selective value.

#### BOURRELETS

Bourrelets are present in the earliest cassiduloids, in which they are slightly to moderately developed, have vertical sides, and bulge slightly into the peristome (e.g., *Clypeus*). By Cenomanian time the bourrelets are often more prominent, as in *Catopygus* or *Ochetes*. They reach the zenith of their development in the Senonian, particularly in the Maestrichtian, when they become very large in such

genera as *Hardouinia*, *Rhynchopygus*, *Lefortia*, *Clypeolampas*, *Fau-raster*, *Domechinus*, and *Hypsopygaster*. In some species such as *Hardouinia porrectus* (Clark) (pl. 21, fig. 5) the bourrelets are huge, and toothlike. After the Maestrichtian, bourrelets are never as well developed, and except for the Eocene *Australanthus longianus* (Gregory) the bourrelets never even approach in size the ones found in the Maestrichtian species.

The function of the bourrelets is to aid the echinoid in food gathering. Bourrelets are covered with many small spines which are used to push food particles up into the mouth.

#### PERIPROCT

In the earliest cassiduloids such as *Clypeus* and *Nuculolites* the periproct is usually supramarginal, often in contact with the apical system. By early Cretaceous time, however, there are many genera with the periproct already marginal or inframarginal such as *Pygaulus*, *Pygorhynchus*, *Astrolampas*, and *Catopygus*. In the Turonian and Cenomanian, most of the genera have marginal or inframarginal periprocts, but in the Senonian with the advent of the Cassidulidae, and in the Tertiary, there are many species again with supramarginal periprocts, but in none of them is the periproct as anterior and near the apical system as in the earliest cassiduloids.

It is obvious why the periproct and anal opening shifted away from the apex of the echinoid. With the development of petals and the subsequent shifting of the respiration function from the gills to them, it was necessary that the anal debris not be discharged over the petals.

#### PERISTOME

In the Jurassic cassiduloids, the peristome is usually slightly anterior, pentagonal, and with the length equal to the width as in *Clypeus*, *Nuculolites*, and *Galeropygus*. In the Early Cretaceous the peristome is either wider than long or very often oblique as in *Pygaulus*, *Pygorhynchus*, and *Pygopistes*. The long axis of this oblique peristome is from left anterior to right posterior. The reason for this obliquity is not known. From the Senonian to the Recent, there are no more species with an oblique peristome, and most of the Late Cretaceous and Tertiary genera have a pentagonal peristome usually wider than high.

## TUBERCULATION

There is a trend in the cassiduloids for a development of a specialized adoral tuberculation differing from the adapical tuberculation. In the Jurassic species, the adoral tuberculation is very similar to the adapical, with tubercles of approximately the same size. By Neocomian time the adoral tubercles near the peristome are slightly larger than the adapical tubercles. In the Cenomanian, the adoral tubercles are considerably larger, and for the first time there is a naked, granular, often pitted sternal area in interambulacrum 5. The large adoral tubercles often have eccentrically situated bosses. In the Late Cretaceous and Tertiary most of the genera have larger tubercles adorally and many have naked sternal areas. The presence or absence of this naked area seems of great significance taxonomically, and it is unfortunate that no Recent cassiduloids have been studied in sufficient detail to learn its function. Probably the larger adoral tubercles and the naked sternal area have a burrowing function. Nichols (1959, p. 417) describes the burrowing use of the adoral spines in the spatangoids.

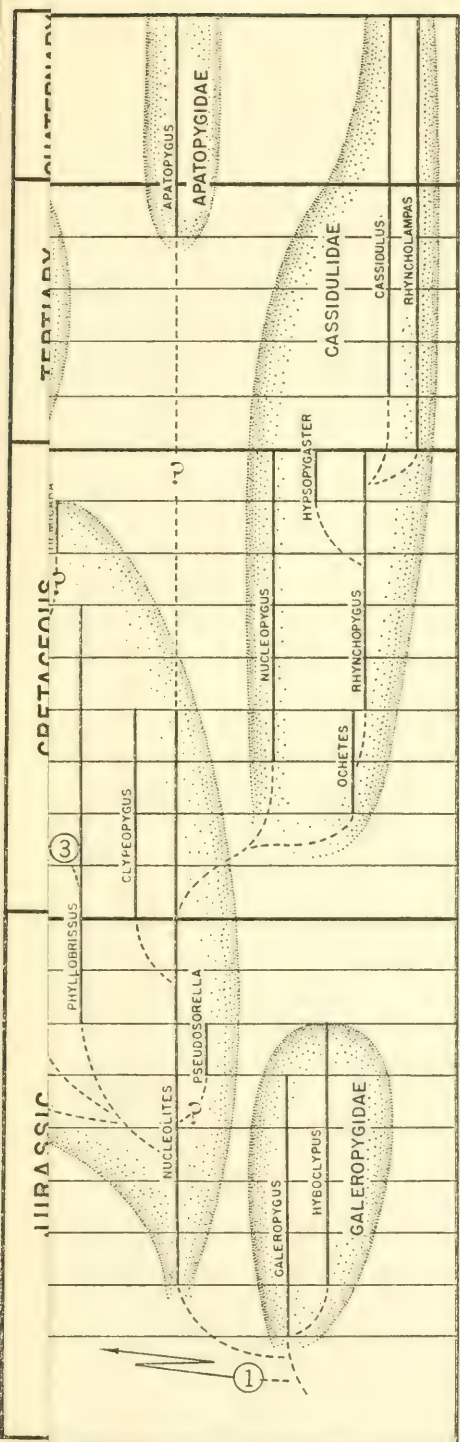
## SHAPE

In the cassiduloids there is a trend toward elongation of the test (chart 4). In many of the earliest genera, e.g., *Clypeus* and *Mepygyrus*, the test outline is circular, and some are wider than long. By the Early Cretaceous, and from that time until the present, most of the genera are elongate. There are some exceptions such as some of the Maestrichtian species of *Hardouinia* which are circular. Generally, the post-Jurassic species that have circular tests are highly inflated, as in some of the larger species of *Echinolampas*, whereas many of the circular Jurassic species are quite low. Presumably the trend toward elongation reflects a change in living habits, probably burrowing, where the elongate test would be better suited for moving through the sediments of the sea bottom.

## SIZE

There is no trend in the size of the test of echinoids. Some Tertiary species are just as large as some Jurassic species. There do seem to be more smaller species in the Upper Cretaceous and Early Tertiary, with large numbers of small species in the Cassidulidae.





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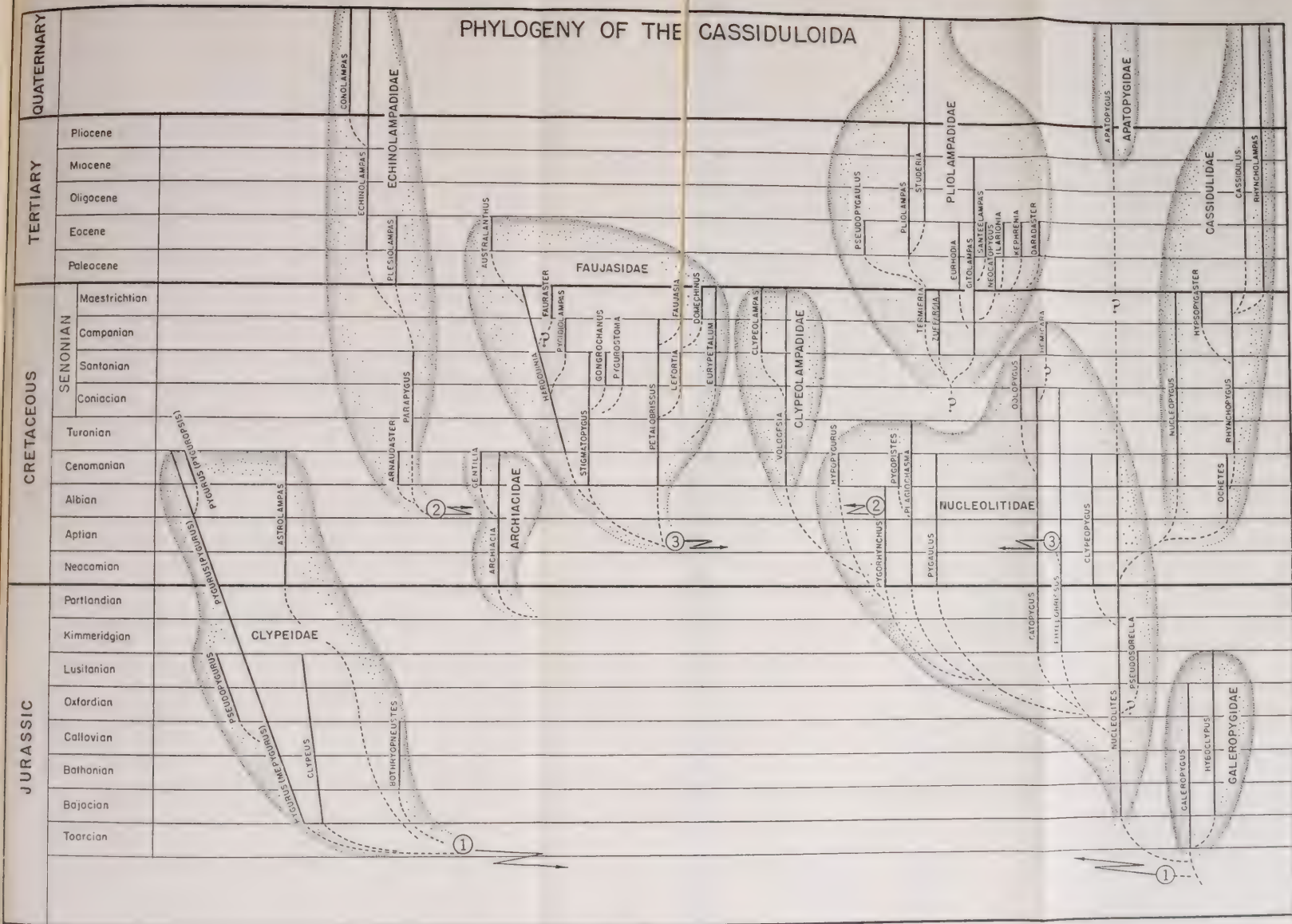


CHART 5.—Phylogeny of the Cassiduloida.



## SUMMARY OF EVOLUTIONARY TRENDS

From a study of the cassiduloids the following evolutionary trends are apparent:

1. The ambulacral plates beyond the petals have double pores in all the pre-Cenomanian species, but single pores in most of the Upper Cretaceous and all the Tertiary species.
2. Buccal pores are introduced at the same time that the double pores are reduced to single pores.
3. The phyllodes become shorter and wider, have fewer pores, and become single pored.
4. There is an increase in the area of test below the petals.
5. The outer poriferous zone in the petals is narrower in the later species.
6. The apical system in the earlier species is tetrabasal, often with complementary and catenal plates. The complementary and catenal plates are lost by the end of the Jurassic, and at the end of the Cretaceous the system becomes monobasal.
7. The bourrelets reach their zenith of development in the Maestrichtian.
8. The periproct is typically supramarginal in the more primitive species.
9. The tubercles become larger adorally, and in the later species a naked area may be present adorally in interambulacrum 5.
10. The shape of the test changes from circular to elongate.

## PHYLOGENY

Using these evolutionary trends as the criteria, it is possible to suggest the phylogeny of the cassiduloid genera (chart 5).

The Galeropygidae are the earliest of all the cassiduloids, and the most primitive in that they have a supramarginal periproct in contact with the apical system, very slightly developed petals, a low, wide test, and long, narrow phyllodes. Within the family, *Ilyboclypus*, which is more advanced in having an elongate test, appears descended from *Galeropygus*.

The Clypeidae are descended from the Galeropygidae or from a close ancestor of the Galeropygidae. They are more advanced as shown by their well-developed petals and usually more marginal or inframarginal periproct. Within the family, *Pseudopygurus*, *Pygurus*, and *Clypeus* are closely related, all three having well-developed petals, a low test, and in the earlier species narrow phyllodes with

crowded pores. There is considerable evolution within *Pygurus*, and the genus is divided into three subgenera, the earlier, more primitive *Pygurus* (*Mepygurus*), the later *Pygurus* (*Pygurus*), and *Pygurus* (*Pyguropsis*). *Pygurus* (*Pygurus*) differs from *Pygurus* (*Mepygurus*) in having shorter, broader phyllodes with fewer pore pairs, a higher test, shorter petals not extending as far adorally, with narrower poriferous zones, and large adoral tubercles. *Pygurus* (*Pyguropsis*) differs from *Pygurus* (*Pygurus*) in having a higher test. *Pseudopygurus* is descended from *Pygurus* and very closely related to it, differing only in having a less developed petal III. *Clypeus* differs from *Pygurus* in having a supramarginal instead of inframarginal periproct, and is probably descended from the same stock that produced *Pygurus*. *Astrolampas* and *Bothryopneustes* are tentatively placed in this family but appear intermediate between it and the Nucleolitidae. *Astrolampas*, because of its low test and wide petals, is allied with *Pygurus*, but the pores in its phyllodes are not crowded, having only two series of pore pairs in each half-ambulacrum, a character common with the Nucleolitidae. In *Bothryopneustes* the petals and the phyllodes are intermediate in development with those typical in the Nucleolitidae and the Clypeidae.

The Nucleolitidae, like the Clypeidae, are descended from the Galeropygidae or a close ancestor of the Galeropygidae. They are more advanced in having more pronounced petals and usually fewer pore pairs in their phyllodes. All the genera in the family, with the possible exception of *Pseudosorella*, appear to be derived from *Nucleolites*. All their phyllodes are very similar in having two series of pore pairs in each half-ambulacrum; most of them have similar, open petals with narrow poriferous zones, and elongate tests. In *Pseudosorella* the phyllodes are similar to those in *Nucleolites*, but the test is very wide, a character found in *Galeropygus*. Of all the genera in the family, *Clypeopygus* has the strongest affinities with *Nucleolites*. Both genera have very similar petals, phyllodes, and position of periproct, and differ only in that *Clypeopygus* has a more depressed test. *Phyllobrissus* is closely related to *Nucleolites*, because both genera have narrow, straight, open petals, and very similar phyllodes, but it appears to be more advanced in having a more elongate test, more developed bourrelets, and a more marginal periproct. *Phyllobrissus* is very similar to *Catopygus* and probably closely related, having similar petals, strikingly similar phyllodes with the inner pore of each pair greatly reduced in size, and well-developed bourrelets. *Catopygus* appears to be slightly more advanced with a



more elongate test and more marginal periproct. *Oolopygus* appears to be a more advanced offshoot of *Catopygus*. It is similar to *Catopygus* in having a small, elongate, moderately inflated test, narrow, equal petals, marginal periproct, and longer than wide peristome. It is more advanced in having single pores in its ambulacral plates beyond the petals, and in having buccal pores. The position of *Hemicara* is not clear. It resembles *Catopygus* in its floscelle and slightly developed petals, but has an inframarginal periproct. *Pygaulus* appears to be an offshoot from *Catopygus*. Both genera have a cylindrical test, and narrow, straight, open, petals extending to the margin. However, the peristome in *Pygaulus* is oblique, and it is not closely allied with *Catopygus*. Both *Pygorhynchus* and *Plagiochasma* are similar to *Pygaulus*. All three genera have the peristome oblique (although some species of *Pygorhynchus* have it regular), open petals with narrow poriferous zones, similar phyllodes, and longitudinal periproct. They differ only in the location of the periproct and shape of test. *Pygopistes* is apparently a direct offshoot from *Plagiochasma* in having the same petal arrangement, an oblique peristome, and similar phyllodes, but being slightly more advanced in having a marginal periproct. *Hypopygurus* appears to be an offshoot of *Pygorhynchus* in having similar petals and the same position of periproct, but it has buccal pores and is therefore more advanced.

The family Faujasidae appears to be descended from the Nucleolitidae, probably from a form similar to *Phyllobrissus*. The evolutionary trend in this family seems to be toward a decrease in the number of pores in the phyllodes, an increase in the development of the bourrelets and petals, and the change from a tetrabasal to monobasal apical system. *Petalobrissus* is similar to *Phyllobrissus* in having the same shape and a supramarginal periproct, but is more advanced in having single pores in the ambulacral plates beyond the petals, buccal pores, stronger bourrelets, and wider outer poriferous zones in the petals. *Hardouinia* originated from an ancestor like *Petalobrissus*. The older species of *Hardouinia* are very similar to some species of *Petalobrissus*, having similar phyllodes, a supramarginal, longitudinal periproct, and a similarly shaped test. They differ only in that the bourrelets are more strongly developed in these species of *Hardouinia* and the periproct is more central. Later species of *Hardouinia* have much wider, shorter phyllodes with even more developed bourrelets, and are easily distinguished from *Petalobrissus*. *Pygidiolampas* is an offshoot from *Hardouinia*, differing

only in having an inframarginal periproct. *Fauraster* may be related to *Hardouinia* in having similar wide petals, a supramarginal periproct, and strong bourrelets, but until something is known of its phyllodes its affinities cannot be determined. *Australanthus* may be descended from *Hardouinia*, having strong bourrelets, wide phyllodes, equal petals, and a supramarginal periproct. It is more advanced as shown by its monobasal apical system. *Stigmatopygus* appears to be descended from the same stock as *Hardouinia*, having a similar large inflated test, supramarginal periproct, broad, closed, equal petals, flat adoral surface, large bourrelets, and broad phyllodes. *Gongrochanus* is probably descended from *Stigmatopygus*, differing from it only in having more pores in its phyllodes and a prominent bulge in the median area of each phyllode. *Pygurostoma* is related to *Gongrochanus*, having wide phyllodes with many pores, strong bourrelets, and well-developed petals. *Lefortia*, *Faujasia*, *Eurypetalum*, and *Domechinus* appear to be related, all having similar broad petals, wide phyllodes, moderately strong bourrelets, and broad tests of medium size, and may be descended from *Petalobrissus*.

Apparently, the Cassidulidae evolved from the Nucleolitidae, with *Nucleopygus* originating from *Nucleolites*. The two genera are similar in having a supramarginal periproct and straight, open petals with narrow poriferous zones, but *Nucleopygus* is more advanced in having single pores in its ambulacral plates beyond the petals and in having buccal pores. *Rhynchopygus* is similar to *Nucleopygus* in its small test and petal arrangement but differs in having stronger bourrelets, wider phyllodes, more advanced tuberculation with larger tubercles adorally, and a naked zone in interambulacrum 5. Both *Ochetes* and *Hypsopygaster* seem more closely related to *Rhynchopygus* than to *Nucleopygus*, sharing with *Rhynchopygus* strong bourrelets, larger tubercles adorally, and a naked pitted zone in interambulacrum 5. Having double pores in its ambulacral plates beyond the petals, *Ochetes* is more primitive than *Rhynchopygus*, whereas *Hypsopygaster* with its monobasal apical system is more advanced than *Rhynchopygus*. *Cassidulus* is very similar and with little doubt a descendent of *Rhynchopygus*, from which it differs only in having a monobasal apical system. *Rhyncholampas* has strong affinities with *Cassidulus* as shown by the existence of some species with characters intermediate between these two genera.

The Echinolampadidae are descended from the Nucleolitidae, probably from a genus like *Pygorhynchus*. The two oldest genera in the family, *Arnaudaster* and *Parapygus*, are very similar to *Pygorhyn-*

*chus*, the only important difference between them being that the ambulacral plates of *Arnaudaster* and *Parapygus* are single pored beyond the petals and they have buccal pores. Because both of these characters are advanced features and both *Arnaudaster* and *Parapygus* occur later than *Pygorhynchus*, it is apparent that *Pygorhynchus* is the ancestor. The stock that produced the *Echinolampas*-*Plesiolampas* group appears to be derived from *Parapygus*. Both *Parapygus* and *Echinolampas* have petals with narrow poriferous zones that are unequal in length in the same petal, transverse, pentagonal mouths, and strong but not pointed bourrelets. *Plesiolampas* and *Echinolampas* are obviously evolved from the same stock inasmuch as they are nearly indistinguishable; differing only in that in *Plesiolampas* the periproct is longitudinal, whereas it is transverse in *Echinolampas*. *Conolampas* is an offshoot from *Echinolampas*, differing only in having straighter petals with narrower poriferous zones.

The Pliolampadidae are not homogeneous and may not represent a natural or phylogenetic grouping. They are distinguished from the Echinolampadidae in having petals with poriferous zones of equal length and in usually lacking a naked zone in interambulacrum 5 adorally. They differ from the Faujasidae in having neither large pointed bourrelets nor very broad phyllodes. They originated from the Nucleolitidae, but it is not clear from what genus. The family can be divided into two morphological and perhaps phylogenetic stocks: one having open petals with very broad poriferous zones, including *Zuffardia*, *Termieria*, *Pliolampas*, *Pseudopygaulus*, and *Studeria*, and the other having closed petals with narrow poriferous zones, including *Gitolampas*, *Eurhodia*, *Ilarionia*, *Neocatopygus*, *Santeelampas*, *Daradaster*, and *Kephrenia*. Among those with broad poriferous zones, *Studeria* greatly resembles *Pliolampas* and probably is descended from it. *Pseudopygaulus* appears to be descended from *Termieria*, both genera having broad petals, oval peristomes, transverse and inframarginal periprocts, similar tuberculation, and phyllodes with few pores. *Pseudopygaulus* differs in having no petal in ambulacrum III. The relationships of the genera of the other stock are not clear, although it appears that they may be offshoots from a *Gitolampas* stock.

The Clypeolampadidae include those genera, *Vologesia* and *Clypeolampas*, with the test large and highly inflated, adoral surface flat, open petals broad and long with wide poriferous zones, and phyllodes with many pores. In shape and size they are very similar to *Echino-*



*lampas* and might be considered ancestral except that their petals have broad, equal poriferous zones, whereas these are narrow and of unequal length in *Echinolampas*. They are distinguished from the Pliolampadidae by their larger, much more inflated tests, longer petals, phyllodes with more pores, and naked zone in interambulacrum 5 adorally. Their origin among the Nucleolitidae is not clear, but they may have sprung from a genus similar to *Hypopygurus*, as they have very similar petals.

The Archiacidae have two series of pores in their phyllodes in each half-ambulacrum, and therefore probably originated from some genus in the Nucleolitidae, but it is not clear from which genus. The two genera in the family, *Archiacia* and *Gentilia*, are closely related, both sharing several unusual characters including the doubling of pores in ambulacrum III and the absence or great reduction of a petal in this ambulacrum. *Gentilia* is more advanced, having single pores in the ambulacra beyond the petals (except in the adapical portion of ambulacrum III), whereas *Archiacia* has double pores.

*Apatopygus*, the only genus in the Apatopygidae, is probably descended from *Nucleolites*. In both genera the petals are straight, narrow, open, with narrow poriferous zones, the periproct is supra-marginal, the test is of a similar shape, bourrelets slightly developed, and the phyllodes have two series of pores in each half-ambulacrum. *Apatopygus* occurs much later and, as would be expected, there are single pores in the ambulacra beyond the petals, whereas in the earlier *Nucleolites* there are double pores. The absence in *Apatopygus* of buccal pores in a single-pored phyllode and the presence of "pyrinid" plating in the ambulacra beyond the petals distinguishes this genus from all the other cassiduloids and casts some doubt on its affinities.

#### DISTRIBUTION IN TIME

The relative abundance of the known cassiduloid species is shown on chart 6. One of the most striking features of this distribution is their great abundance in the Eocene and their subsequent decrease in the upper Tertiary and Quaternary. Over 500 species have been reported from the Tertiary, but there are only 16 species living today. Part of this great Eocene expansion is more apparent than real. Because most of the earlier workers did not distinguish the Paleocene from the Eocene, some of their species may belong to the Paleocene.

The great decline in species may have been caused by a cooling of the seas and an increase in competition from other echinoids. Evidently the cassiduloids are almost restricted to warm water, as shown

		WITHIN ORDER	
QUATERNARY			
TERTIARY	Pliocene		
	Miocene		
	Oligocene		
	Eocene		
	Paleocene		
CRETACEOUS	Maestrichtian		
	Campanian		
	Santonian		
	Coniacian		
	Turonian		
	Cenomanian		
	Albian		
	Aptian		
	Neocomian		
JURASSIC	Portlandian		
	Kimmeridgian		
	Lusitanian		
	Oxfordian		
	Callovian		
	Bathonian		
	Badenian		
	Toarcian		





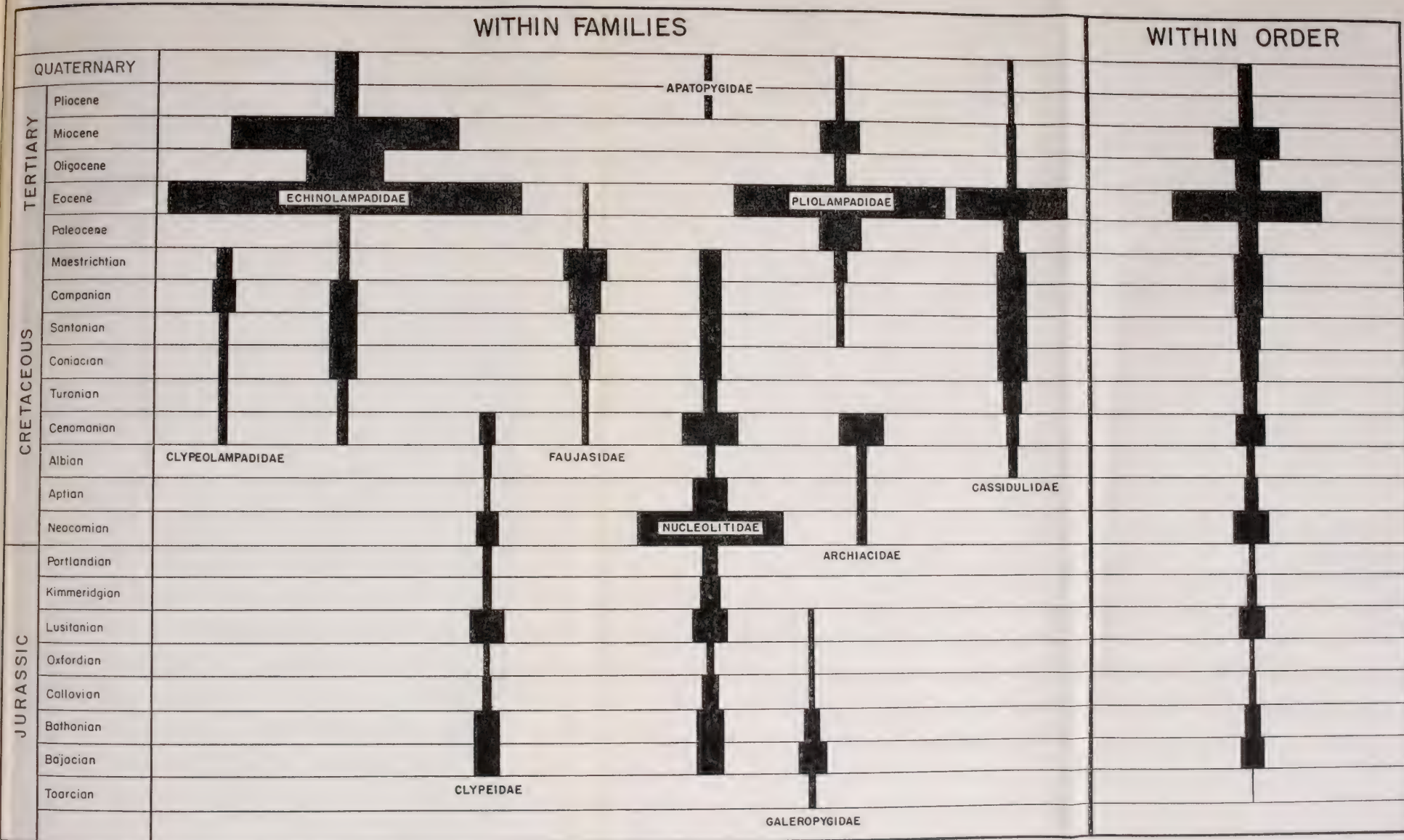


CHART 6.—Distribution in time of the Cassiduloida.



by the occurrence of almost all the living species in tropical waters and of most of the Tertiary species in rocks believed to have been deposited in tropical seas. According to Durham (1959, p. 9) the Paleocene-Eocene tropical zone was much broader than it is today, gradually contracting since the Eocene. This contraction may explain the decrease in the cassiduloids, not only because it reduced the area where they lived, but also because it may have increased the competition between them and other animals occupying a similar niche. It is probably significant that the great decrease in the number of cassiduloids occurred at the same time as an increase in the number of spatangoids and clypeastroids.

### ECOLOGY

Unfortunately, the ecology of none of the recent species of cassiduloids has been studied. The only information of any significance is A. Agassiz's (1873, p. 555) statement that *Rhyncholampas pacificus* (Agassiz) "lives like other spatangoids of which the habits are known, gregariously on sandy beaches, from five to six feet below low-water mark, half buried in the sand up to the extremities of the petals." I have tried to locate in the Western Hemisphere a living population of cassiduloids that I could study, but with no success. *Cassidulus cariboeorum* Lamarck lives in the Caribbean, but neither I nor any of the many marine biologists that I have contacted have seen them in any numbers. Dr. Lowell P. Thomas at the Marine Laboratory at the University of Miami reported (personal communication) that he had found one live specimen of *C. cariboeorum* on a sandy bottom in about 18 inches of water at Lameshur Bay, St. John, Virgin Islands, but no observation was made on whether the specimen was buried or not. Fred Ziesenhenné reports (personal communication) that he dredged up from 10 fathoms over 100 specimens of *Rhyncholampas pacificus* 175 miles northeast of Cape San Lucas, Baja California, Mexico. These specimens came from a sandy bottom, but Mr. Ziesenhenné could not observe how they lived because of the depth of the water. He states that he has never taken them in tangles, which would indicate that they do not live on the surface of the sand. Other than this information, nothing is known of the living habits of the cassiduloids. It is hoped that someone will make a study of the cassiduloids similar to the magnificent work done by Nichols (1959) on the spatangoids.

From a study of the morphology of the cassiduloids it can be conjectured that they lived only partially buried up to their petals.

Although spatangoids breathe with petals, they are able to live completely buried because they have fascioles that create currents, driving air-laden water over the petals and a specially adapted anterior ambulacrum with long tube-feet to maintain an open burrow to the surface. Both these structures are lacking in the cassiduloids.

Among the fossil cassiduloids, species of *Hardouinia* evidently lived in a littoral environment. *H. mertonis* and *H. porrectus* are found in great numbers in a sandstone at the top of the Ripley formation. Dr. Norman F. Sohl, who has done extensive work on this formation, states (personal communication) that the echinoids occur with a typical heavy-shelled littoral molluscan assemblage including *Idonearca littlei* (Gabb), *Aphrodina* sp., *Pachycardium* sp., *Tellina* sp., *Ostrea* cf. *O. subspatulata* Forbes, and *Cyprimeria*. According to Dr. Sohl, this coarse sandstone appears from its texture, sedimentary structures, and facies relationships to be a littoral beach deposit formed in a high-energy environment. Littoral currents as well as strong wave action probably agitated the sediments continuously during the time of deposition. *H. mertonis* appears to be well adapted to this environment. Its high test enabled the echinoid to live partially buried in the sand with only its petals exposed. The covering by sand of the nonpetaloid marginal portion of the test would serve to anchor the echinoid and lessen the possibility of its being flipped over by currents. The heavy, jutting bourrelets would aid in keeping a passage open through the sand for the passing of food from the phyllodal tube-feet to the mouth.

#### SYSTEMATICS

In order to avoid unnecessary duplication, I have not included for any of the genera a synonymy of previous work or a history of previous workers' opinions on the taxonomy of the suprageneric taxa. This information is readily available in Mortensen's (1948) great monograph.

#### Order CASSIDULOIDA Claus, 1880

Circular to elongate; apical system tetrabasal or monobasal; ambulacra petaloid adapically; periproct outside of apical system; phyllodes and usually bourrelets present; no jaws or gill slits in adult.

*Comparison with other orders.*—The cassiduloids are distinguished from the holotypoids by their usually elongate shape, petaloid ambulacra, presence of phyllodes and usually bourrelets, and absence of



a lantern in any adults. They differ from the spatangoids in lacking fascioles, in not having a specialized plastron, and in having a floscelle.

*Remarks.*—Durham and Melville (1957, p. 260) divided the Cassiduloida into two orders: the Nucleolitida and the Cassiduloida. All the genera with tetrabasal apical system and unequal pores in the petals were placed in the Nucleolitida, and all with monobasal apical system and nearly equal pores in the petals were placed in the Cassiduloida. This division, however, is not feasible, for there are many genera such as *Clypeolampas*, *Kephrenia*, *Pliolampas*, *Gitolampas*, *Rhyncholampas*, and *Australanthus* which have a monobasal apical system but have the pores of their petals very unequal. As a matter of fact, there are more genera with a monobasal apical system and unequal pores than with equal pores. If this biordinal classification were used, many genera which are very similar in other characters would be separated into different orders. *Cassidulus* would not be in the same order as its very close relative *Rhynchopygus*, even though both genera differ only in that one has a tetrabasal apical system, whereas the other is monobasal. At one time I thought that the Cassiduloida could be separated into two orders on the presence of one or two pores in the ambulacral plates beyond the petals and in the phyllodes. However, this division would be artificial, being purely morphological and not phylogenetic. Many genera closely related in the sum total of their characters would be placed in separate orders. *Parapygus* and *Pygorhynchus* would be placed in different orders even though they are indistinguishable except for the presence of single pores in *Parapygus*. Likewise *Gentilia* would be separated from *Archiacia*, *Rhynchopygus* from *Ochetes*, and *Oolopygus* from *Catopygus*.

#### Family GALEROPYGIDAE Lambert, 1911

Large, circular to elongate; apical system central, tetrabasal; peri-proct supramarginal, in contact with apical system, longitudinal, in deep groove extending to posterior margin; peristome anterior, oval; ambulacra subpetaloid, flush with test, open, long, extending almost to margin; all ambulacral plates double pored; bourrelets absent or slightly developed; phyllodes narrow, double pored with two or three series of pore pairs in each half-ambulacrum; no buccal pores; tubercles adorally slightly larger than adapically; no naked, granular zone in interambulacrum 5.

*Genera.*—*Galeropygus*, *Hyboclypus*.

*Range.*—Jurassic (Toarcian to Rauracian).

*Remarks.*—The Galeropygidae are distinguished from the Nucleolitidae by having subpetaloid ambulacra instead of the well-developed and often broad petals found in the Nucleolitidae.

This family concept coincides with Lambert and Thiéry's (1921, p. 336), but not with Mortensen's (1948, p. 101), whose use of the family is far broader. He includes the genera *Loriolella*, *Desorella*, *Galeroclypeus*, *Infraclypeus*, and *Menopygus*, but all these genera lack phyllodes and usually petals and should not be referred to any family in the Cassiduloida.

#### Genus GALEROPYGUS Cotteau

*Galeropygus* Cotteau, 1856. Bull. Soc. Géol. France, ser. 2, vol. 13, p. 648. Type species by original designation, *Hyboclypus agariciformis* Wright.  
Synonym: *Ressopygus* Pomel.

#### GENERIC DESCRIPTION

Medium to large size, low or domed, circular; apical system tetra-basal, genital plates forming semicircle around adapical border of periproct; petals slightly developed, narrow, all ambulacral plates double pored; periproct in contact with apical system, longitudinal, groove leading from opening to posterior margin; peristome anterior; bourrelets slightly developed; phyllodes double pored with many pore pairs arranged in three series; no buccal pores; tubercles perforate, crenulate, not arranged in vertical series, slightly larger on adoral surface.

*Comparison with other genera.*—*Galeropygus* is very similar to *Hyboclypus*, having slightly developed petals, its periproct in contact with the apical system, and similar phyllodes with numerous pore pairs arranged in three series in each half-ambulacrum. It differs in having a broad apical system with the genital plates arranged in a semicircle, whereas in *Hyboclypus* the system is elongate with genital plates 2 and 3 usually separated from plates 1 and 4 by ocular plates II and IV. Furthermore, in *Galeropygus* the bourrelets are slightly developed, but are absent in *Hyboclypus*.

*Range and distribution.*—Jurassic (Toarcian to Oxfordian) of Europe.

#### DESCRIPTION OF TYPE SPECIES

#### GALEROPYGUS AGARICIFORMIS (Wright)

Plate 1, figures 1-4; text figure 2

*Hyboclypus agariciformis* Wright, 1851. Ann. Mag. Nat. Hist., ser. 2, vol. 9, p. 99.

*Material*.—Two specimens studied in the U. S. National Museum collections, one in the École National Supérieure des Mines, Paris, and nine in the British Museum (Natural History).

*Shape*.—Medium to large size; outline varying from circular, to wider than high, flattened, with low, smoothly domed adapical surface, slightly depressed adoral surface; ambulacra on adoral side slightly depressed.

*Apical system*.—Central, tetrabasal, genital plates arranged in semicircle anterior to opening of periproct.

*Ambulacra*.—Petals very slightly developed (pl. 1, fig. 4), posterior petals flexuous; all petals extending almost to margin; pores not conjugate; outer pore slightly elongated transversely, inner round.

*Periproct*.—Supramarginal, in contact with apical system, longitudinal, with groove extending from opening to posterior margin.

*Peristome*.—Anterior, slightly pentagonal.

*Floscelle*.—Bourrelets slightly developed; phyllodes (text fig. 2) double pored with many pore pairs, arranged in three series in each half-ambulacrum, with six or seven pore pairs in each series; no buccal pores.

*Tuberculation*.—Tubercles perforate, crenulate, not arranged in vertical series; slightly larger adorally than adapically.

*Occurrence*.—Middle Jurassic (Bajocian to Bathonian) of England and France.

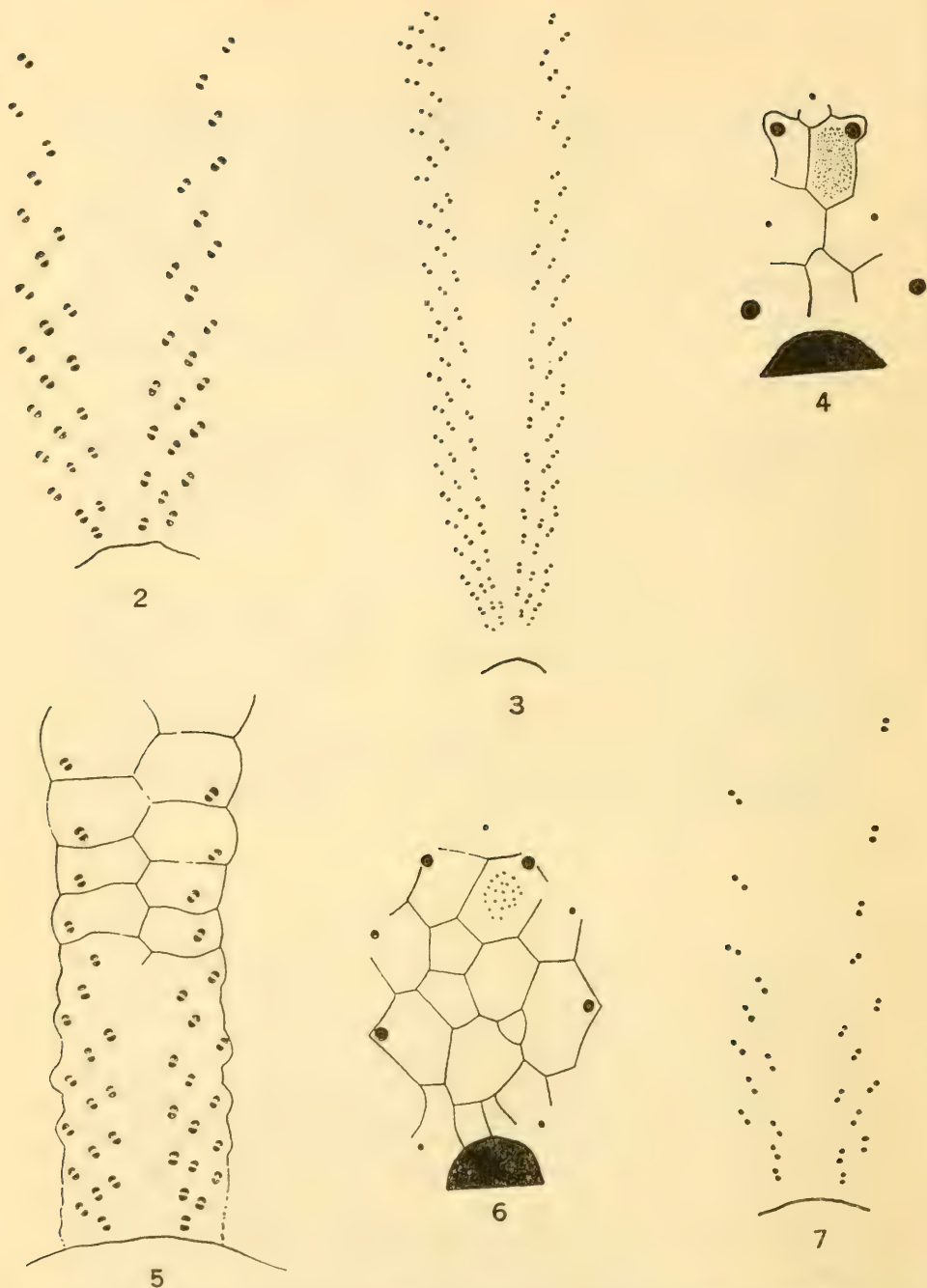
*Location of type specimen*.—Unknown.

#### Synonym of *GALEROPYGUS*

*Ressopygus* Pomel, 1883. *Class. méth.*, p. 56. Type species by subsequent designation, Mortensen (1948, p. 109), *Clypeus constantini* Cotteau.

*Remarks*.—I found a topotypic specimen of this species in the Lambert Collection at the Sorbonne, Paris. The specimen is not well preserved but the phyllodes are visible, and a drawing of one of them is included in text figure 3. Since this specimen shows no features not visible on Cotteau's (1873, *Pal. franc., Jur.*, pl. 63) original figures, I do not include a description of it.

Both Lambert and Thiéry (1921, p. 336) and Mortensen (1948, p. 109) considered *Ressopygus* a synonym of *Galeropygus*. The type species of both genera are very similar, each having a large broad test, with narrow ambulacra, slightly developed petals, phyllodes with many pore pairs arranged in three series, and a supramarginal periproct in contact with the apical system. They differ in that in *G. constantini* petals V and I distally curve posteriorly, whereas in



FIGS. 2-7.—2, *Galeropygus agariciformis* (Wright): Phylloide of ambulacrum III of USNM 19561, from Jurassic (Inferior Oolite) at Cheltenham, England,  $\times 10$ . 3, *Galeropygus constantini* (Cotteau): Phylloide of ambulacrum IV of topotypic specimen in Lambert Collection, Sorbonne, Paris, from Jurassic (Bajocian) at Les Tremardieres, Poitiers, France,  $\times 15$ . 4, 5, *Hyboclypus gibberulus* Agassiz: 4, Apical system of specimen in Museum of Comparative Zoology, Harvard, from Jurassic (Inferior Oolite) at Broad Windsor, England,  $\times 4$ . Many of the plate sutures were not visible. 5, Phylloide of ambulacrum II of specimen in Lambert Collection, Sorbonne, Paris, from Jurassic (Bathonian) at Amberieux (Ain) France,  $\times 10$ . 6, 7, *Hyboclypus caudatus* Wright: 6, Apical system of Wright's (1856, pl. 22, fig. 2h) figured specimen from the Inferior Oolite in the British Museum (B.M.E. 1505), magnification not known; 7, phylloide of ambulacrum V of specimen in Lambert Collection, Sorbonne, Paris, from Cheville (Sarthe), France,  $\times 15$ .



*G. agariciformis* they curve anteriorly. This difference is not of sufficient significance to warrant generic distinction.

Genus **HYBOCLYPUS** L. Agassiz

*Hyboclypus* L. Agassiz, 1839. Éch. foss. Suisse, vol. 1, p. 75. Type species by monotypy, *Hyboclypus gibberulus* L. Agassiz.

Synonym: *Aulacopygus* Pomel.

GENERIC DESCRIPTION

Medium to large size, flattened; apical system tetrabasal, elongate, oculars II and IV usually in contact; petals slightly developed, all ambulacral plates double pored; periproct in contact with apical system, in longitudinal groove continuing to posterior margin; peristome anterior; no bourrelets, phyllodes double pored with many pairs of pores in three rows on each side; no buccal pores; tubercles slightly larger adorally than adapically.

*Comparison with other genera.*—*Hyboclypus* is very similar to *Galeropygus*. In both genera the petals are slightly developed, the periproct is in contact with the apical system, and the phyllodes have many pore pairs arranged in three series in each half-ambulacrum. It is distinguished by having an elongate apical system with oculars II and IV usually separating genital plates 2 and 3 from 1 and 4, whereas in *Galeropygus* the system is broad with the genital plates arranged in a semicircle around the anterior margin of the periproct. Furthermore, in *Hyboclypus* there are no bourrelets, whereas they are slightly developed in *Galeropygus*.

*Range and distribution.*—Jurassic (Bajocian to Rauracian) of Europe.

DESCRIPTION OF TYPE SPECIES

**HYBOCLYPUS GIBBERULUS** L. Agassiz

Plate 1, figures 6, 7; text figures 4, 5

*Hyboclypus gibberulus* L. Agassiz, 1839. Éch. foss. Suisse, vol. 1, p. 75, pl. 12, figs. 10-12.

*Material.*—Two specimens studied in the Lambert Collection, at the Sorbonne, 1 in the Muséum National d'Histoire Naturelle, Paris, and 17 at the British Museum (Natural History).

*Shape.*—Medium to large, round to elongate, varying with specimens, generally low except for high ridge extending from apical system toward anterior margin; depressed around peristome, interambulacra inflated, ambulacra depressed.



*Apical system*.—Slightly anterior, tetrabasal (text fig. 4) oculars II and IV in contact separating genital plates 2 and 3 from genital plates 1 and 4; complementary plates present in some specimens.

*Ambulacra*.—Petals slightly developed, long, extending to margin, widely open with very broad interporiferous zones, four or five times width of poriferous zones; petals V and I with slight curve; outer pore of pair elongate transversely, inner pore round, conjugate.

*Adoral interambulacra*.—Two series of low, alternating plates; in interambulacrum 5 plates larger than in other areas.

*Periproct*.—Supramarginal, opening in contact with apical system, longitudinal with groove continuing from opening to posterior margin.

*Peristome*.—Anterior, depressed, oval longitudinally.

*Floscelle*.—No bourrelets; phyllodes (text fig. 5) double pored with many pairs of pores arranged in three series in each half-ambulacrum, five or six pairs of pores in each series; phyllodes not expanded; no buccal pores.

*Occurrence*.—Middle Jurassic (Bajocian to Bathonian) of France and England.

*Location of type specimens*.—According to Lambert and Jeannet (1928, p. 126) the type specimens are at the Museum of Carlsruhe.

*Remarks*.—Mortensen considered that the ambulacra were not petaloid. However, the pores on the adapical side are not the same size or shape as those on the adoral side. Adapically, they are large and unequal, the outer being transversely elongate. Adorally they are much smaller, equal, and in peripodia. Furthermore, the pore pairs on the adoral side decrease in size near the margin.

#### Synonym of **HYBOCLYPUS**

*Aulacopygus* Pomel, 1883, *Class. méth.*, p. 53. Type species by monotypy, *Hyboclypus caudatus* Wright.

#### DESCRIPTION OF TYPE SPECIES

#### **HYBOCLYPUS CAUDATUS** Wright

Plate I, figure 5; text figures 6, 7

*Hyboclypus caudatus* Wright, 1851. *Ann. Mag. Nat. Hist.*, ser. 2, vol. 9, p. 100, pl. 3, fig. 2.

*Material*.—The holotype and 16 other specimens including a figured specimen were studied in the British Museum (Natural History); four specimens were seen in the Lambert Collection at the Sorbonne, Paris, and one in the U. S. National Museum.

*Shape*.—Small, average specimen 20 mm. long, elongate, anterior margin gently rounded or slightly blunted, posterior slightly pro-

longed, truncated at anal groove; adorally, inflated anteriorly, sloping posteriorly; adapically, peristome depressed, interambulacra slightly inflated, ambulacra slightly depressed.

*Apical system*.—Anterior, elongate, tetrabasal, with four genital pores situated in distal corners of plates (text fig. 6); genital plates 2 and 3 separated from genitals 4 and 1 by oculars II and IV and several complementary plates. In British Museum specimen B.M.E. 1505, seven complementary plates; number of such plates probably quite variable.

*Ambulacra*.—Petals slightly developed, open, extending over two-thirds distance to margin, petals II, III, and IV straight, petals V and I curved convexly, posteriorly; poriferous zones narrow, pores oblique, inner pore of pair distal to outer; interporiferous zones wide, increasing in width distally.

*Adoral interambulacra*.—Two series of low, alternating plates; in interambulacrum 5 plates larger than in other areas.

*Periproct*.—Supramarginal, in contact with apical system, longitudinal, in deep triangular groove increasing in width toward posterior margin.

*Peristome*.—Anterior, higher than wide, oval to subpentagonal.

*Poroscelle*.—Bourrelets slightly developed; phyllodes double pored, with slight crowding of pore pairs (text fig. 7), no buccal pores.

*Tuberculation*.—Tubercles perforate, crenulate, slightly larger on adoral surface than adapical.

*Occurrence*.—Middle Jurassic (Bajocian–Bathonian) of England and France.

*Location of type specimen*.—Holotype in British Museum (Natural History), No. B.M.E. 1579.

*Remarks*.—*H. caudatus* has been considered generically or subgenerically distinct from *Hyboclypus* because of its apical system, which is elongate with complementary plates separating oculars II and IV, and genital plates 1 and 4. In *Hyboclypus* the apical system is also elongate and the complementary plates usually separate genital plates 1 and 4, but not completely oculars II and IV. I do not believe that this difference in apical system is of generic significance. The arrangement and number of complementary plates is very variable even within one species. In *Hyboclypus gibberulus*, according to Cotteau's (1873, Pal. franc., Jur., pl. 93, figs. 7, 9) figures, in one specimen there is only one complementary plate with both genital plates 1 and 4 and oculars II and IV in contact, and in another specimen there are three complementary plates separating genitals 1 and 4 and partially oculars II and IV.

Wright's (1856, pl. 22, fig. 2h) figure of the apical system in *H. caudatus* is incorrect. I have studied the same specimen under high magnification and include (text fig. 6) a drawing of its apical system. There are seven complementary plates instead of two, and oculars II and IV are much larger than shown in Wright's figure. Mortensen (1948, p. 115) also found large oculars in a specimen he collected of this species.

#### Family CLYPEIDAE Lambert, 1898

Usually large, low, broad, with flat adoral surface; apical system anterior, tetrabasal, always four genital pores; periproct usually longitudinal; peristome anterior, pentagonal; petals usually broad, closed, of equal length, outer pores slitlike, strongly conjugate, all ambulacral plates double pored; bourrelets well developed; phyllodes in early species usually with three series of pore pairs in each half-ambulacrum, in later, only one; no buccal pores; in later species adoral tubercles larger than adapical, no naked granular zone in interambulacrum 5.

*Genera*.—*Clypeus*, *Bothryopneustes*, *Pygurus*, *Astrolampas*, *Pseudopygurus*.

*Range*.—Jurassic (Bajocian) to Cretaceous (Cenomanian).

*Remarks*.—The Clypeidae are most similar to the Nucleolitidae, but differ in usually having a lower, broader, larger test, broader petals with broad outer poriferous zones, and phyllodes with more pore pairs. *Pygurus* and *Pseudopygurus* are distinct from any other genera in the Nucleolitidae, but *Astrolampas* and *Bothryopneustes* have characters intermediate between the Clypeidae and Nucleolitidae and consequently blur the distinction between the two families. *Astrolampas* has the shape and wide petals of a clypeid, but the phyllodes of a nucleolitid, and in *Bothryopneustes* the petals and phyllodes are intermediate between those typical within the two families. Most of the species of *Clypeus* have a wider, lower, and larger test, wider petals with broader outer poriferous zones and longer, more crowded phyllodes than in any nucleolitid, but there are a few species in which these distinctive characters are not so well developed.

#### Genus CLYPEUS Leske

*Clypeus* Leske, 1778. Klein's Nat. dispos. ech., p. 93. Type species herein designated *Clypeus plotii* Leske.

Synonyms: *Auloclypeus* Pomel; *Crotoclypeus* Pomel; *Dactyloclypeus* Mac-cagno; *Echinoclypeus* de Blainville.

## GENERIC DESCRIPTION

Large, circular, or with blunt anterior margin, pointed posterior as in *Clypeus rostratus* Agassiz, low or medium height, adoral surface depressed or flat; apical system, central or posterior to center, tetrabasal, posterior ocular plates posteriorly prolonged, extending to periproct, or short, sometimes with catenal plates joining apical system to periproct; petals long, broad, open, with broad, tapering poriferous zones, outer pore slitlike, all ambulacral plates double pored; periproct supramarginal, in groove or flush; peristome pentagonal, slightly anterior to center; bourrelets well developed, phyllodes double pored, with three series of pore pairs in each half-ambulacrum; no buccal pores.

*Comparison with other genera.*—In petal arrangement and phyllode structure, *Clypeus* is very similar to *Pygurus* (*Mepygurus*), but is distinguished from it by its supramarginal periproct. It differs from *Nucleolites* in having wider petals with broader poriferous zones, usually a wider test, and much longer and more crowded phyllodes with three series of pore pairs in each half-ambulacrum instead of the two in *Nucleolites*. There are, however, some species that are intermediate in some of these characters, and it is difficult to know to which of the two genera to refer them.

*Remarks.*—Many authors have indicated that *C. plotii* is the type species of *Clypeus*, but all of them considered Klein (1734) as the author of the genus. Since Klein is pre-Linnaeus, their designation of a type species has no validity.

I have studied one specimen of *Clypeus rostratus* L. Agassiz from the Naturhistorisches Museum at Basel, Switzerland, in which two complementary plates occur in the apical system (text fig. 8) posterior to genital 2 and anterior to the posterior oculars. Having seen only one specimen, I do not know whether or not these plates are typical in *C. rostratus*. I have included a figure (text fig. 9) of a phyllode of this specimen, and of a specimen of *Clypeus altus* M'Coy (text fig. 10) studied in the École des Mines, Paris.

*Range and distribution.*—Jurassic (Bajocian to Rauracian) of Europe, Africa.

## DESCRIPTION OF TYPE SPECIES

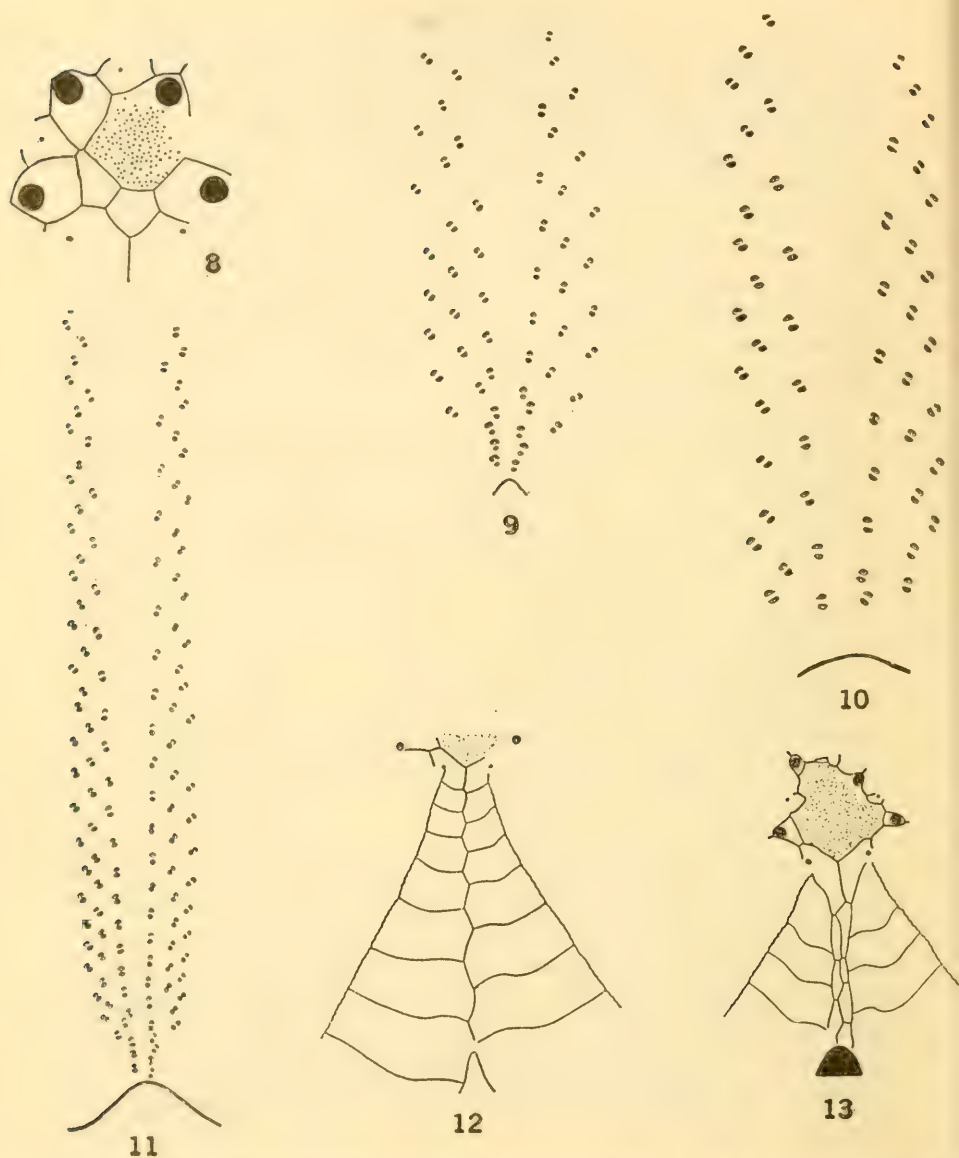
**CLYPEUS PLOTII** Leske

Plate 7, figure 6

*Clypeus plotii* Leske, 1778. Klein's Nat. dispos. ech., p. 93.

*Material.*—Sixteen specimens studied in the collections of the U. S. National Museum, two in the Museum of Comparative Zoology, Harvard.





FIGS. 8-13.—8, 9, *Clypeus rostratus* Agassiz: 8, Apical system  $\times 8$ , and 9, phyllode of ambulacrum III,  $\times 8$ , of specimen in the Naturhistorisches Museum, Basel, Switzerland, from the Middle Jurassic (Bathonian) Variansschichten, Aargauer, Jura, Switzerland. 10, *Clypeus altus* M'Coy: Phyllode of ambulacrum III of specimen in École National Supérieure des Mines in Paris, from Dorsetshire, England,  $\times 10$ . 11-13, *Clypeus agassizi* (Wright): 11, Phyllode of ambulacrum V of specimen in Museum of Comparative Zoology, Harvard, from Middle Jurassic (Bathonian), Upper Inferior Oolite, Broad Windsor, Dorset, England,  $\times 4$ ; 12, adapical view of interambulacrum 5, showing lack of catenal plates in same specimen,  $\times 8$ ; 13, adapical view of interambulacrum 5 showing catenal plates in USNM Springer Collection 54984, from same locality,  $\times 8$ .



*Shape*.—Large, flattened, circular, greatest height at center, anterior to apical system, adoral surface flat or depressed.

*Apical system*.—Posterior to center, tetrabasal (text fig. 14 for *C. sinuatus*), madreporite large, extending posteriorly to posterior oculars, greatly separating posterior genital plates, other genital plates small, triangular, pore in genital plate 3 more anterior than pore in genital plate 2. Posterior oculars prolonged posteriorly, extending to opening of periproct.

*Ambulacra*.—Petals broad, long, extending to margin, open. Petals II, III, IV, longer than V, I. Petals V, I curving slightly distally in some specimens. Interporiferous zones slightly wider than poriferous zones; poriferous zones very wide, outer pore of pore pair slitlike, very elongated, inner pore slightly elongated obliquely.

*Adoral interambulacra*.—Two plates at peristome in each interambulacrum preceded by regularly alternating plates.

*Periproct*.—Supramarginal, in contact with posterior oculars, elongated longitudinally, in deep groove which extends to posterior margin.

*Peristome*.—Slightly anterior, pentagonal.

*Floscelle*.—Bourrelets strongly developed, inflated. Phyllodes (text fig. 15 for *C. sinuatus*) double pored, extremely long, extending two-thirds length of ambulacrum on adoral side, with many pore pairs arranged in three series in each half-ambulacrum: approximately 15 pore pairs in each series.

*Tuberculation*.—Tubercles on adoral surface larger than on adapical surface.

*Occurrence*.—Jurassic (Bajocian and Bathonian) of England, France, Switzerland.

*Location of type specimen*.—Unknown.

*Remarks*.—Wright (1859, p. 363), Cotteau (1870, Pal. franc., Jur., p. 192), and others have considered that Leske's *C. plotii* and *C. sinuatus* are synonyms. The specimens referred to *C. plotii* came from the Inferior Oolite in the *Clypeus* grit, which is uppermost Bajocian, resting directly under the Zig Zag beds which Cifelli (1959, p. 269) considers lowermost Bathonian. *C. sinuatus* is supposedly from the Bathonian Greater Oolite. The specimens I have studied from the Greater Oolite are smaller (pl. 7, figs. 1, 2; pl. 8, fig. 4), have a more depressed adoral surface, and posterior petals curving distally, as opposed to the Inferior Oolite specimens (pl. 7, fig. 6) with a large test, flat adoral surface, and straight posterior petals. Probably these specimens represent two separate species, the large

Greater Oolite form *C. sinuatus*, and the smaller Inferior Oolite form *C. plotii*. I do not have sufficient specimens available to make a decision, and hope that an English paleontologist will reexamine all the specimens in the British collections and collect additional material in order to tie in this material stratigraphically. It is probable that an interesting evolutionary trend would be discovered.

#### Synonym of CLYPEUS

*Auloclypeus* Pomel, 1883. Class. méth., p. 60. Type species, *Nucleolites michelini* Wright, by subsequent designation, Mortensen (1948, p. 130).

*Remarks.*—I have not seen any specimens of the type species of this genus, but from a study of Cotteau's (1872, Pal. franc., Jur., pl. 57) figures, it appears to be a *Clypeus*. Mortensen (1948, p. 130) provisionally referred it to *Clypeus* but because of its short posterior oculars thought it might be referred to *Echinobrissus* (= *Nucleolites*). However, not all the species of *Clypeus* have long posterior oculars; for example, in some specimens of *Clypeus agassizi* these oculars are short. Furthermore, the test in *C. michelini* is much larger, broader, and lower than in *Nucleolites*.

#### Synonym of CLYPEUS

*Crotoclypeus* Pomel, 1883. Class. méth., p. 60. Type species by subsequent designation, Lambert and Thiéry, 1921, p. 344, *Nucleolites agassizii* Wright.

#### DESCRIPTION OF TYPE SPECIES

##### CLYPEUS AGASSIZI (Wright)

Plate 5, figure 5, plate 8, figure 1; text figures 11-13

*Nucleolites agassizi* Wright, 1851. Ann. Mag. Nat. Hist., ser. 2, vol. 9, p. 368, pl. 3, figs. 3a-c.

*Material.*—Two specimens studied, one in the Museum of Comparative Zoology, Harvard; the other in the U. S. National Museum.

*Shape.*—Extremely large, circular in outline, inflated adapical surface, greatest height slightly anterior to center, flat adoral surface.

*Apical system.*—Slightly posterior to center, tetrabasal, madreporite very large, other genital plates small; oculars V and I in contact, in some specimens prolonged. Catenal plates joining apical system to periproct present or absent (text figs. 12, 13).

*Ambulacra.*—Petals broad, long, extending to margin, petals II, III, IV longer than V, I. Interporiferous zones slightly wider than poriferous, petals open. Poriferous zones very wide owing to great width of outer pore, narrowing at extremities of petals. Pores conjugate, outer very slitlike, inner slightly elongated.

*Periproct.*—Supramarginal, midway between apical system and

posterior margin, in slight groove extending from apical system to posterior margin. Opening longitudinal.

*Peristome*.—Anterior, pentagonal.

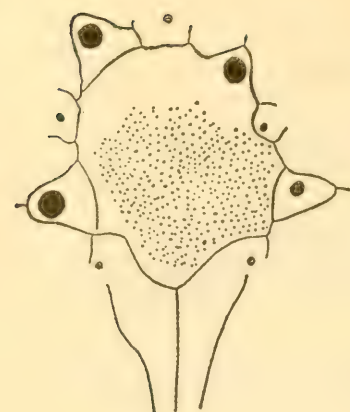
*Phylloscelle*.—Bourrelets well developed, inflated. Phyllodes not widened (text fig. 11), double pored, very long, extending almost to margin, pore pairs arranged in three series in each half-ambulacrum; no buccal pores.

*Occurrence*.—Jurassic (Bajocian) of England and France.

*Location of type specimen*.—Probably in the British Museum (Natural History).

*Remarks*.—The two specimens I studied came from the same locality and are without doubt the same species, but their apical systems are not similar. In one, there are no catenal plates joining the apical system to the periproct, and in the other the catenal plates are numerous and the posterior oculars are prolonged (see text figs. 12, 13). The presence of catenal plates is a variable feature in this species and is obviously not of as great taxonomic importance as has been considered.

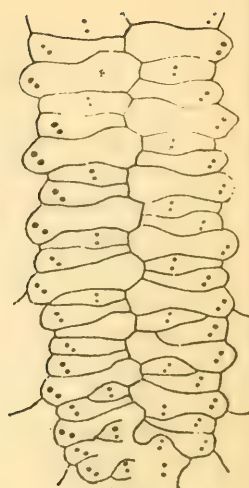
Pomel stated that this genus differed from *Clypeus* in having shorter posterior ocular plates, and in having the periproct more distant from the apical system. He referred three species to the genus, *Clypeus hugi* Agassiz, *Nucleolites agassizi* Wright, and *Echinites subulatus* Young and Bird. Lambert and Thiéry (1921, p. 344) maintained the genus as described by Pomel, but later (1925, p. 586) restricted the genus to species having the apical system joined to the periproct by a series of plates. They transferred *C. hugi* and *E. subulatus* to *Clitopygus*. The short posterior ocular plates, however, and the small plates joining the apical system to the periproct are not valid generic characters, because they are variable within the type species. The two specimens I studied of *Clypeus agassizi* came from the same locality and are similar in all respects except that in one the posterior oculars are short and there are no plates joining the apical system to the periproct (text fig. 12), but in the other the posterior oculars are very long and are joined to the periproct by a series of plates (text fig. 13). Furthermore, I have found this same variation in specimens of *Nucleolites scutatus* (text figs. 30-32). *C. agassizi* has strikingly similar petals, peristome, bourrelets, and phyllodes to those of the type species of *Clypeus*, *C. plotii*, and differs only in having a more inflated test, and its periproct more distant from the apical system and not in a deep groove. These differences do not warrant generic separation, and *Crotoclypeus* is herein considered a junior subjective synonym of *Clypeus*.



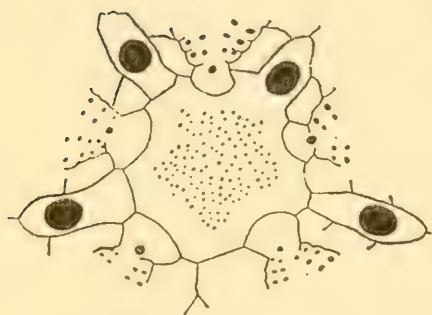
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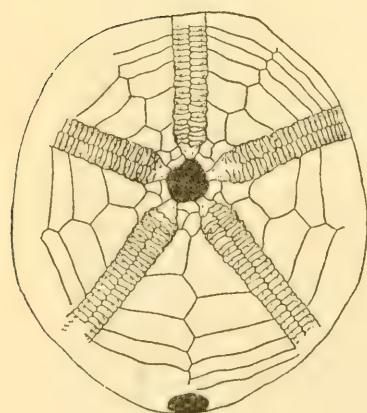
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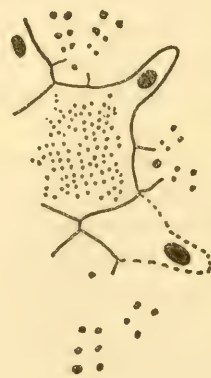
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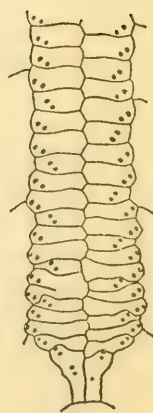
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FIGS. 14-20.—14, 15, *Clypeus sinuatus* Leske: 14, Apical system of USNM 131253, from the Middle Jurassic (Bathonian), Great Oolite, at Kirtlington, Oxford, England,  $\times 8$ ; 15, phyllode of ambulacrum I of specimen No. 1037 in the Museum of Comparative Zoology, Harvard, from the Great Oolite, Boulogne sur Mer, France,  $\times 4$ . 16, 17, *Clypeus wylliei* var. *pentagona* Currie: 16, Phyllode of ambulacrum I of Currie's (1925, pl. 10, fig. 2) figured specimen in the Hunterian Museum, Glasgow, from the Jurassic, Bihendula, British Somaliland,  $\times 10$ ; 17, apical system of same specimen,  $\times 10$ . 18-20, *Bothryopneustes lamberti* Fourtau: 18, Adoral view of paratype, USNM 131262, from Upper Jurassic (Callovian), at Gebel Oum Chabba, Egypt,  $\times 3$ ; 19, apical system, partially preserved,  $\times 15$ ; 20, phyllode of ambulacrum II of same specimen.



Mortensen (1948, p. 137) considered *Crotoclypeus* as a synonym of *Hardouinia*. The great difference in the phyllodes of these genera rule out any possibility that they could be synonyms. In *Crotoclypeus* the phyllodes are double pored with the pore pairs arranged in three series in each half-ambulacrum, the phyllodes are not widened, and there are no buccal pores. In *Hardouinia*, the phyllodes are greatly widened, single pored, with the pores arranged in an arc, and with buccal pores. *Hardouinia* is much more advanced.

Lambert and Thiéry (1925, p. 586) restricted *Crotoclypeus* to species having the apical system joined to the periproct by a series of plates. However, this feature is not of generic value but is variable within the type species, as described above.

#### Synonym of CLYPEUS

*Dactyloclypeus* Maccagno, 1947. Atti. Accad. Naz. Lincei Mem., ser. 8, vol. 1, p. 126. Type species herein designated, *Clypeus wylliei* Currie.

#### DESCRIPTION OF TYPE SPECIES

##### CLYPEUS WYLLIEI Currie

Plate 7, figures 3-5; plate 8, figures 2, 3; text figures 16, 17

*Clypeus wylliei* Currie, 1925. Monogr. Geol. Dept. Hunterian Mus., Glasgow Univ., pt. 5, Jur. and Eocene Ech., p. 63, pl. 10, figs. 1, 2.

*Material*.—All four specimens in Currie's original collection, including the type of her variety *pentagona*.

*Shape*.—Medium size, 45 mm. long, circular to pentagonal with width equal to length, adapically moderately inflated with greatest height at apical system, petals slightly inflated; adorally flat to slightly depressed around peristome.

*Apical system*.—Central, tetrabasal (text fig. 17), genital 2 much larger than other genital plates, extending posteriorly, separating posterior genital and ocular plates. Other genital plates very narrow, elongated.

*Ambulacra*.—Petals very broad, open, equal length, extending to margin; poriferous zones very wide, tapering distally, outer pore of pair slitlike, inner round to slightly elongated transversely, joined by deep conjugation groove; interporiferous zones expanding distally.

*Periproct*.—Supramarginal, longitudinal, in groove extending to posterior margin.

*Peristome*.—Anterior, pentagonal, width approximately equal to length.

*Floscelle*.—Bourrelets well developed, vertically sided. Phyllodes



not widened (text fig. 16), very long, double pored, with many pore pairs arranged in three series in each half-ambulacrum, outer two series close to each other almost forming one series; no buccal pores.

*Tuberculation*.—Tubercles on adoral surface slightly larger than on adapical.

*Occurrence*.—Jurassic (Bathonian or Callovian) of British and Italian Somaliland.

*Location of type specimen*.—Hunterian Museum, University of Glasgow, Scotland.

*Remarks*.—Maccagno erected *Dactyloclypeus* as a new subgenus of *Clitopygus* (herein considered a synonym of *Nucleolites*). However, in the type species of *Clitopygus*, *Nucleolites lorioli* (Cotteau), and of *Nucleolites*, *N. scutatus*, the phyllodes are much shorter than in *C. wylliei* with far fewer pore pairs, arranged in only two series, and the petals are much narrower having narrower poriferous zones. Maccagno distinguished *C. wylliei* from *Clypeus* because its periproct is not adjacent to the apical system and because of the character of its bourrelets. There are species of *Clypeus*, however, in which the periproct is not in contact with the apical system, and the bourrelets in *C. wylliei* are very similar to those in the type species of *Clypeus*, *C. plotii* Leske. As originally done by Currie, *C. wylliei* should be referred to *Clypeus*.

#### Synonym of CLYPEUS

*Echinoclypeus* De Blainville, 1830. Dict. Sci. Nat. (Zoophytes), vol. 60, p. 189.

Type species herein designated, *Galerites patella* Lamarck, 1816 (= *Clypeus plotii* Leske, 1778).

De Blainville evidently had not seen Leske's paper, since all the species he referred to *Echinoclypeus*, Leske had also referred to *Clypeus*.

#### Genus BOTHRYOPNEUSTES Fourtau

*Bothryopneustes* Fourtau, 1924. Cat. invertébrés foss. l'Égypte, terr. Jurassiques, pt. 1, Échinodermes, p. 27. Type species by subsequent designation, Currie, 1927, p. 425, *Bothryopneustes lamberti* Fourtau.

Synonym: *Clypeobrissus* Currie.

#### GENERIC DESCRIPTION

Medium, circular to elongate, posterior margin often slightly pointed, adapically moderately inflated, margins well rounded, adorally usually pulvinate with ambulacra depressed; apical system central to slightly anterior, tetrabasal; petals long, extending to margin, wide,

open or slightly closed, equal length, petaloid pores conjugate, outer pore slitlike, all ambulacral plates double pored; periproct marginal to inframarginal, oval, longitudinal, with slight groove extending adorally; peristome slightly anterior, pentagonal, width equal to length, bourrelets well developed; phyllodes slightly broadened, long, double pored, with two or three series of pore pairs in each half-ambulacrum; no buccal pores; tubercles on adoral surface slightly larger than on adapical.

*Comparison with other genera.*—*Bothryopneustes* is very similar to *Clypeus*, having the same petal arrangement and shape of test, and similar floscelle. It differs from *Clypeus* in having its periproct marginal to inframarginal, whereas it is supramarginal in *Clypeus*. Furthermore, the test is usually smaller in *Bothryopneustes*. As an example of the great similarity of the two genera, Currie's *Clypeus wylliei* (pl. 8, figs. 2, 3) and *Bothryopneustes somaliensis* (pl. 9, figs. 7-10), both from the same bed in British Somaliland, are almost indistinguishable except for the location of the periproct.

*Remarks.*—Lambert (1932, p. 184) referred his *Phyllobrissus jourdyi* to *Bothryopneustes*, but its petals are only slightly developed, not broad as typical in this genus.

*Range and distribution.*—Jurassic (Bathonian to Callovian) of Africa and Madagascar.

#### DESCRIPTION OF TYPE SPECIES

##### **BOTHRYOPNEUSTES LAMBERTI** Fourtau

Plate 9, figures 1-4; text figures 18-20

*Bothryopneustes lamberti* Fourtau, 1924. Cat. invertèbrés foss. l'Égypte, terr. Jurassiques, pt. 1, Echinodermes, pp. 28-29, pl. 2, fig. 5.

*Material.*—Holotype and five paratypes studied.

*Shape.*—Small to medium, 16 to 30 mm. long, elongate, anterior margin blunted, posterior slightly pointed, greatest width posterior to center, low, adorally peristome, ambulacra depressed.

*Apical system.*—Slightly anterior, tetrabasal (text fig. 19), genital plates pointed at extremities.

*Ambulacra.*—Petals broad, open to slightly closed, long, extending to margin, interporiferous zones wide, at greatest width almost twice width of poriferous zones, slightly inflated; poriferous zones narrowing distally, petaloid pores conjugate, outer pore greatly elongated transversely, slitlike, inner pore slightly elongated.

*Adoral interambulacrum.*—Single plate at peristome (text fig. 18) preceded by double series of alternating plates.

*Periproct*.—Marginal to slightly inframarginal, longitudinal, oval, higher than wide, slight groove extending adorally.

*Peristome*.—Anterior, depressed, pentagonal, width equal to height.

*Floscelle*.—Bourrelets well developed, inflated, sides oblique; phyllodes (text fig. 20) long, slightly broadened, double pored; in small specimens pore pairs in two series in each half-ambulacrum, approximately 10 pore pairs in each outer series, 4 or 5 in each inner; in large specimens, pore pairs in three series; no buccal pores.

*Tuberculation*.—Adorally tubercles slightly larger than adapically.

*Occurrence*.—Upper Jurassic (Callovian), Gebel Oum Chabba, Egypt.

*Location of type specimen*.—Geological Museum, Cairo, Egypt.

*Remarks*.—I have studied the holotype and two paratypes of Fourtau's (1924, p. 27) *Pyguropsis lorioli* (borrowed from the Geological Museum, Cairo), and after cleaning the holotype I am convinced that this species is certainly congeneric with *Bothryopneustes lamberti*, and probably conspecific. Fourtau considered this species to be a *Pyguropsis* because its periproct is marginal to inframarginal, and created his new genus *Bothryopneustes* for *B. lamberti* because he had the mistaken impression that the periproct in the latter species was supramarginal. Actually the periproct in *B. lamberti* and *B. lorioli* is in the same position—marginal to inframarginal. The holotype of *B. lorioli* differs from the holotype of *B. lamberti* only in appearing to have its outer petaloid pores more slitlike. This difference is not real but reflects the difference in the preservation of the two specimens: the holotype of *B. lamberti* is badly weathered with the outer pores greatly enlarged. The phyllodes, which are visible in two of the paratypes of *B. lorioli* have three series of pore pairs in each half-ambulacrum, whereas only two occur in the types of *B. lamberti*. This difference is probably due to the difference in the size of the specimen. The largest specimen that Fourtau referred to *B. lamberti*, in which the phyllodes were visible, is 24.5 mm. long, and the smallest that he referred to *B. lorioli* is 30 mm. It is to be expected that the phyllodes in the larger specimen would have more pore pairs. Two of Fourtau's paratypes of *B. lorioli* have thicker tests with steeper sides than the holotype of the same species, and evidently are similar to the specimens that Lambert (1932, p. 184) saw when he distinguished *B. lorioli* from *B. lamberti* on the grounds that the test in *B. lorioli* is thicker. This difference in thickness of test may be a variable feature within the species, or these paratypes may represent a separate species. Photographs of the holotype of

*B. lorioli* are included on plate 9, figure 5, 6. Both species were collected at the same locality, and it appears that Fourtau referred the smaller specimens to one species and the larger to another.

#### Synonym of *BOTHRYOPNEUSTES*

*Clypeobrissus* Currie, 1925. Monogr. Geol. Dept. Hunterian Mus., Glasgow Univ., pp. 69-70. Type species by original designation, *Clypeobrissus somaliensis* Currie.

*Remarks.*—Currie was unaware of Fourtau's *Bothryopneustes* when she erected a new genus for her species *Clypeobrissus somaliensis*. Fourtau's paper had just come out shortly before hers. Later (1927, p. 425), she considered her species congeneric with *B. lamberti*, and *Clypeobrissus* a synonym of *Bothryopneustes*. I have studied the type specimen of *B. lamberti* and paratypes of *B. somaliensis* and agree that they are congeneric. Currie's description is very thorough, and no redescription is necessary here, but photographs (pl. 9, figs. 7-10) are included.

Maccagno (1947, p. 129) considered *B. somaliensis* a synonym of *B. orientalis* Fourtau. I have studied a specimen of *B. orientalis*, and its test is much more elongate than in *B. somaliensis*. I include photographs of this specimen on plate 9, figures 11, 12.

#### Genus *PYGURUS* Agassiz

*Pygurus* L. Agassiz, 1839. Éch. foss. Suisse, vol. 1, p. 68. Type species by subsequent designation, Savin, 1902, p. 271, *Echinolampas montmollini* Agassiz. Synonym: *Echinopygus* d'Orbigny.

#### GENERIC DESCRIPTION

Large, often flattened, in some species width greater than length, in others less than length, posterior margin prolonged in some species, greatest height at apical system; apical system tetrabasal, posterior genital plates separated by genital 2, posterior oculars usually in contact, four genital pores; petals broad, equal, or with petal III shorter than others, open or with tendency to close, with wide interporiferous zones, wide tapering poriferous zones with conjugate pores, outer pore slitlike, all ambulacral plates double pored; periproct infra-marginal, longitudinal or transverse; peristome anterior, pentagonal, width greater than or less than height; bourrelets well developed, phyllodes slightly widened, or very broad, double pored, with from one to three series of pore pairs in each half-ambulacrum; no buccal pores.



*Comparison with other genera.*—*Pygurus* is most similar to *Clypeus*, but differs in having an inframarginal periproct.

*Remarks.*—There has been considerable controversy over whether or not *Mepygurus* was distinctive enough from *Pygurus* to warrant generic separation. Beurlen (1933, p. 72) and Mortensen (1948, p. 136) considered *Mepygurus* as a subgenus of *Pygurus*. Beurlen suggested that *Mepygurus* was more primitive than *Pygurus*, but Mortensen disagreed. The study of the phyllodes (see p. 7) shows Beurlen to be correct. The species shown in chart 3 (p. 8) from the Bajocian to Callovian are species that Lambert and Thiéry refer to *Mepygurus*. They have more primitive phyllodes than the species occurring later that are referred to *Pygurus* (*Echinopygus* in Lambert and Thiéry). Furthermore, species referred to *Mepygurus* have in general a lower, broader test, a more central apical system, and broader outer poriferous zones in their petals. However, *Mepygurus* and *Pygurus* are so similar in their general appearance, and so closely related, that it is advisable to maintain Beurlen's and Mortensen's consideration of *Mepygurus* as a subgenus of *Pygurus*. If *Mepygurus* is considered as a distinct genus, its close relationship to *Pygurus* might be overlooked. Furthermore, there are some species which are intermediate between the two subgenera. Lambert's (1905b, p. 575) *Pygurus perreti* has the low, circular shape of a *Mepygurus* but the broadened phyllodes of a *Pygurus*, and could not be referred with certainty to either one of the subgenera.

*Evolution.*—There is a remarkably consistent trend in the evolution of the phyllodes in *Pygurus*, with a broadening of the phyllodes, a reduction in the number of pore pairs, and an increase in the distance between the pores and the edge of the peristome. This trend is described and illustrated in detail on page 8, chart 3.

Besides this evolution in the phyllodes, there are several other trends in *Pygurus*. The outer pores of the petals are much less elongated transversely in the later species than in the earlier. In the Bathonian specimens of *P. depressus* the outer pore is greatly elongated into a narrow slit (pl. 2, fig. 2), and a similar slitlike outer pore occurs in *P. blumenbachi* (pl. 3, fig. 4) from the Lusitanian. In the Neocomian species, *P. rostratus* Agassiz, and *P. montmollini* (Agassiz) (pl. 2, fig. 1) the outer pores are less elongated. This trend reaches its maximum in the Albian and Cenomanian species, *P. jagueyanus* Cooke, *P. lampas* (De la Beche) (pl. 3, fig. 1), and *P. africanus* De Loriol, in which the outer pore is much less elongated than in the earlier species.



The tubercles are larger on the adoral surface of the later species than they are on the earlier. In *P. depressus* (pl. 2, fig. 5) of the Bathonian, and the Callovian *Pygurus* (*Mepygurus*) sp. from Madagascar the tubercles are quite small, whereas in the Albian *P. jagueyanus* and the Cenomanian *P. lampas* (pl. 3, fig. 2), they are much larger. There is a trend toward a narrower test, with most of the earlier species such as *P. depressus* and *P. blumenbachi* having a wide test with the width exceeding the length, and most of the later having a more elongate test with the length exceeding the width as in *P. lampas* and *P. africanus*. However, there are exceptions to this trend, with such species as *P. acutus* Agassiz from the Bajocian having an elongate test, and *P. royeri* Cotteau from the Kimmeridgian having a very wide test.

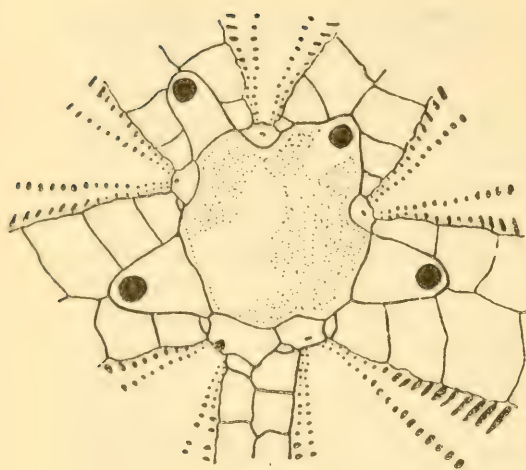
In general, in later species the test is higher than in the earlier. In the Bajocian species *P. acuta* and *P. terquemii* the height is approximately 25 percent of the length, whereas in the Albian *P. jagueyanus* it is 34 percent and in the Cenomanian *P. lampas* it is 58 percent.

As discussed above (see p. 10), the petals in the earlier species extend to the margin of the test, but in the later species they terminate at a considerable distance adapical to the margin.

*Ecology.*—Joysey (1952), in a most interesting paper, has given his interpretation of the ecology of *Pygurus hausmanni* (Koch and Dunker). From a study of the tubercles and the petals, he has concluded that *P. hausmanni* lived partially buried with its lower surface completely covered with sediment, and its petals free of sediment.

*Morphology.*—On the holotype, in the Lambert Collection at the Sorbonne, of *P. geryvillensis* Peron and Gauthier, there are four unusual pores in each phyllode. These pores occur between the edge of the peristome (chart 3, fig. e) and the first pore pairs of the phyllode in the position of buccal pores, and are probably primitive buccal pores. As discussed on page 7, buccal pores, with this one exception, do not occur in the cassiduloids until the Cenomanian, and then usually only in species having single-pored phyllodes.

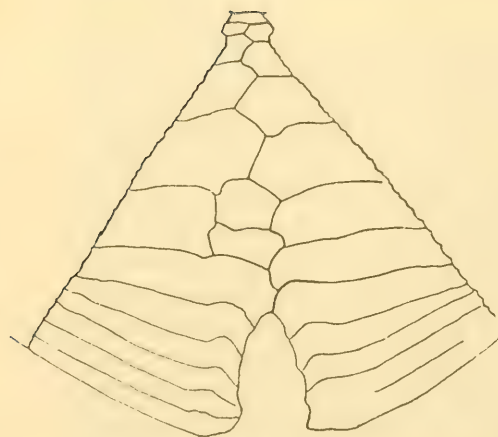
M. Collignon very kindly lent me 21 specimens of an undescribed species of *Pygurus* (*Mepygurus*) from Madagascar. Most of the specimens are beautifully preserved, showing clearly the plate sutures. It is interesting to note that in some of the specimens the posterior oculars are in contact (text fig. 21) as is typical in the genus, but in others these oculars are separated by one interambulacral plate (text



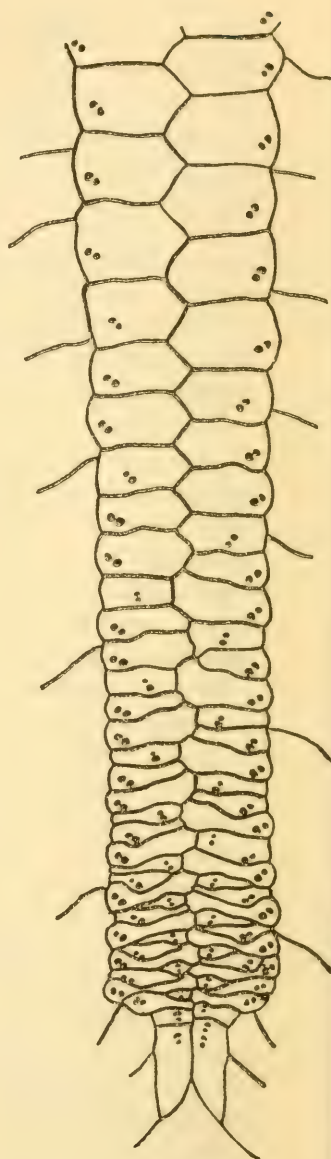
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FIGS. 21-24.—*Pygurus* (*Mephygurus*) sp.: 21, 22, Apical system,  $\times 5$ ; 23, view of adoral interambulacrum 5 showing several plates inserted in series,  $\times 1.3$ ; 24, phyllode of ambulacrum III,  $\times 8$ , from specimens in Collignon Collection, from Besavoa, Madagascar.

fig. 22). In interambulacrum 5 of two specimens, there are one or two plates on the adoral surface inserted between (text fig. 23) the regular plates of the interambulacrum. As the plate sutures are usually not clear in the phyllodes, I have included (text fig. 24) a drawing of a phyllode in which most of the sutures are visible.

*Remarks.*—Cooke (1955, p. 98) transferred his *Faujasia chelonium* to *Pygurus*. Having single-pored phyllodes and a monobasal apical system, this species is not a *Pygurus*, but is referred below (p. 141) to a new genus.

*Range and distribution.*—Middle Jurassic (Bajocian) to Cretaceous (Cenomanian) of worldwide distribution.

#### Subgenus PYGURUS Agassiz

*Type species.*—*Echinolampas montmollini* Agassiz.

*Remarks.*—This subgenus includes those species of *Pygurus* that have a slightly elongate, somewhat inflated test, an anterior apical system, broad, depressed phyllodes with from three to one series of pore pairs in each half-ambulacrum, and with the first pore pairs in a phyllode widely separated from the edge of the peristome. This subgenus is more advanced than *Pygurus* (*Mepygurus*).

*Range.*—Jurassic (Oxfordian) to Cretaceous (Cenomanian).

#### DESCRIPTION OF TYPE SPECIES

##### PYGURUS (PYGURUS) MONTMOLLINI (Agassiz)

Plate 2, figure 1; chart 3, figure h

*Echinolampas montmollini* L. Agassiz, 1836a. Mém. Soc. Sci. Nat. Neuchâtel, vol. 1, p. 134, pl. 14, figs. 4-6.

*Material.*—Five specimens were seen in Paris, two in the Muséum National d'Histoire Naturelle, and three in the École des Mines. The floscelle and peristome was not visible on any of these specimens.

*Shape.*—Large, broad, width slightly greater than length, with greatest width slightly posterior to center; slight, broad anterior groove, posterior margin slightly pointed, lobed on either side; adapical surface inflated with greatest height at apical system; adoral surface pulvinate with interambulacra swollen, ambulacra depressed, area around periproct flattened.

*Apical system.*—Anterior, tetrabasal, genital plates large, extending posteriorly, separating posterior genital plates; posterior oculars in contact.

*Ambulacra.*—Petals broad, equal, closed, long, petal III extending

almost to margin, petals II and IV two-thirds to margin, petals V and I between one-half and two-thirds distance to margin; interporiferous zones very wide, tapering distally; poriferous zones wide with outer pore slitlike, inner pore slightly elongated transversely, pores conjugate.

*Periproct*.—Inframarginal, longitudinal with anterior side of opening slightly pointing, posterior blunt; in slight, flat groove extending one-third distance from periproct to peristome.

*Peristome*.—Anterior, pentagonal, width slightly less than height.

*Floscelle*.—Not exposed on any specimens studied by this author, with following description based on illustrations by d'Orbigny (1856, pl. 917, figs. 1, 4) and Cotteau (1860 [1857-1878], pl. 59, fig. 6; Yonne). Bourrelets well developed; phyllodes large (chart 3, fig. h), greatly broadened, depressed, with two series of double pores in each half-ambulacrum, approximately 13 pore pairs in each outer series, 6 in each inner; no buccal pores; pore series terminate at considerable distance from edge of peristome.

*Occurrence*.—Lower Cretaceous (Neocomian) of France and Switzerland.

*Location of type specimen*.—According to Lambert and Jeannet (1928, p. 177) the holotype is at the Institut de Géologie at Neuchâtel, Switzerland.

### Synonym of PYGURUS (PYGURUS)

*Echinopygus* d'Orbigny, 1856. Pal. franc., Crétacé, vol. 6, p. 303. Type species, *Clypeaster oviformis* var. 2 Lamarck=*Echinoaus lampas* De la Beche by subsequent designation, Lambert and Thiéry (1921, p. 355).

### DESCRIPTION OF TYPE SPECIES

#### PYGURUS (PYGURUS) LAMPAS (De la Beche)

Plate 3, figures 1-3; chart 3, figure k

*Echinoaus lampas* De la Beche, 1833. Trans. Geol. Soc., ser. 2, vol. 1, p. 42, pl. 3, figs. 3-5.

*Material*.—Three specimens were studied in the École des Mines, Paris. One of these is the specimen figured by De la Beche, according to its label. This specimen is herein designated the lectotype.

*Shape*.—Large, lectotype 74.0 mm. long, length greater than width, margin angular with posterior greatly prolonged, adoral surface inflated with greatest height anterior to center at apical system and with steeply sloping sides; greatest width posterior to center; adoral surface concave.



*Apical system*.—Anterior, tetrabasal, with four genital pores.

*Ambulacra*.—Petals broad, equal, long, extending over two-thirds distance to margin, closed, with very wide interporiferous zones, strongly tapering distally. Poriferous zones narrow, inner pores slightly elongated transversely, outer pores slitlike.

*Periproct*.—Inframarginal, on slight oblique truncation, tear-drop shaped, with apex pointing adorally, width approximately equal to length.

*Peristome*.—Anterior, pentagonal, slightly higher than wide.

*Floscelle*.—Bourrelets strongly developed, toothlike. Phyllodes double pored, very broad and large, deeply depressed between bourrelets; one series of pore pairs in each half-ambulacrum (chart 3, fig. k) with wide space between series; pore pairs widely separated from edge of peristome; no buccal pores.

*Tuberculation*.—Tubercles on adoral surface larger than those on adapical surface.

*Occurrence*.—Cretaceous (Cenomanian) at Coulaines, Caniculus à Yore, Le Mans, and Fouras in France, and Lyme, England.

*Location of type specimen*.—Lectotype in École des Mines, Paris.

*Remarks*.—d'Orbigny established this genus for the species *P. (Pygurus) lampas* and *P. (Pygurus) rostratus* and distinguished *Echinopygus* from *Pygurus* on just one character: the periproct is transverse in *Echinopygus* but longitudinal in *Pygurus*. Desor (1857, p. 310) and Cotteau (1867, Pal. franc., Jur., p. 128) considered that this difference was not of sufficient importance to warrant generic distinction. Lambert and Thiéry (1921, p. 355) did not consider the periproct to be transverse and considered the two genera to be synonymous, but because they thought the name *Pygurus* was preoccupied, they substituted *Echinopygus* for *Pygurus*. Mortensen (1948, p. 133) pointed out correctly that the name *Pygurus* was available to Agassiz because Dejean's (1833) *Pygurus* was a nomen nudum. Mortensen disagreed with Lambert and Thiéry and stated that the periproct was transverse in *P. lampas* and cited d'Orbigny's (1856, pl. 919, fig. 2) figure in which the periproct is shown as being much wider than high. From my own observation of specimens of *P. lampas*, the width of the periproct is approximately equal to the length. In *P. rostratus*, however, the periproct is definitely wider than high. However, it is so similar in all its other characters to the type species of *Pygurus* (*Pygurus*), *P. montmollini*, that I believe it should be considered as congeneric with *Pygurus*.



### Subgenus **MEPYGURUS** Pomel

*Mcpygurus* Pomel, 1883. Class. méth., p. 65. Type species, *Pygurus michelini* Cotteau, 1849=*Pygurus depressus* Agassiz in Agassiz and Desor, 1847, by subsequent designation, Lambert and Thiéry (1921, p. 356).

*Description*.—This subgenus includes all those species of *Pygurus* that have a low, broad test, with a central or slightly anterior apical system, slightly depressed and not broadened phyllodes with three or four series of pore pairs in each half-ambulacrum, and with the first pore pairs in a phyllode near the edge of the peristome.

*Range*.—Jurassic (Bajocian to Oxfordian).

#### DESCRIPTION OF TYPE SPECIES

#### **PYGURUS (MEPYGURUS) DEPRESSUS** Agassiz

Plate 2, figures 2-5; text figure 25; chart 3, figure a

*Pygurus depressus* Agassiz in Agassiz and Desor, 1847. Ann. Sci. Nat., Zool., ser. 3, vol. 7, p. 162.

*Pygurus michelini* Cotteau, 1849. Éch. foss., L'Yonne, vol. 1, p. 70, pl. 5, fig. 7.

*Material*.—Three specimens were studied in the Museum of Comparative Zoology at Harvard, one in the U. S. National Museum, and four in the École des Mines in Paris, including two specimens figured by Cotteau (1869, pl. 31, figs. 1-3).

*Shape*.—Large, up to 84 mm. in length, shape variable, in some specimens length greater than width, in others less than width; anterior margin often blunt, posterior margin often pointed, greatest width central or posterior to center; test low, flattened, with greatest height at apical system or anterior to it; adoral surface depressed, pulvinate, with interambulacra inflated, ambulacra depressed.

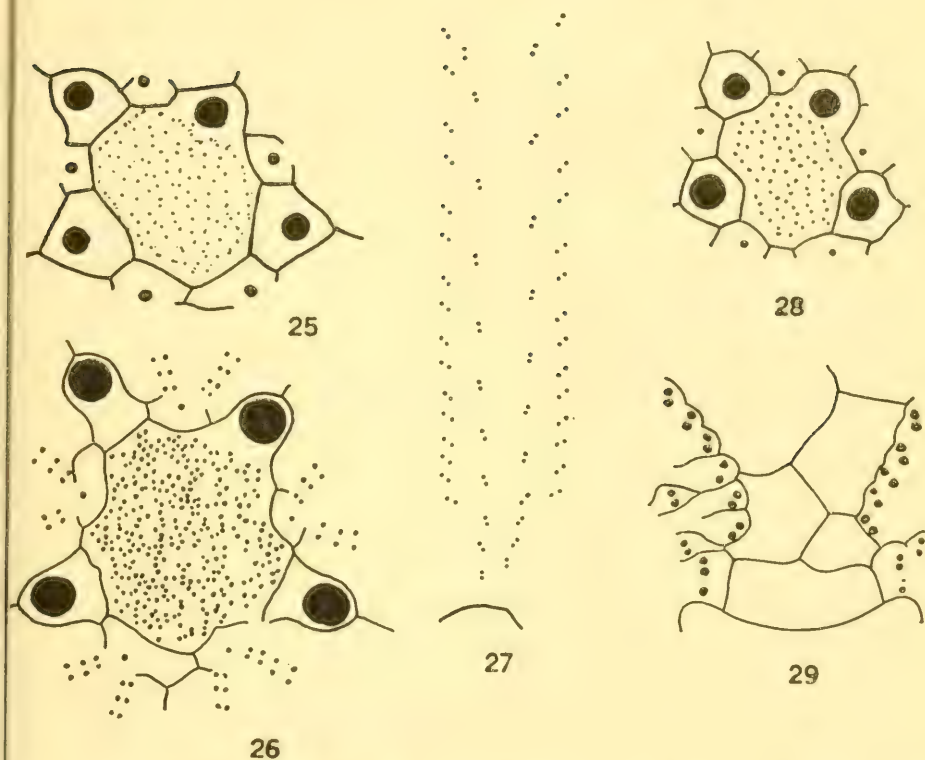
*Apical system*.—Central or slightly anterior, tetrabasal, genital 2 large, extending posteriorly, separating posterior genital plates (text fig. 25), posterior ocular plates in contact.

*Ambulacra*.—Petals equal, broad, closed, long, extending almost to margin; interporiferous zones very wide, tapering distally; poriferous zones wide with outer series of pores elongated into broad slits, inner pores slightly elongated transversely, pores conjugate; poriferous zones tapering distally.

*Periproct*.—Inframarginal, longitudinal, tear-drop shaped with apex pointing adorally; in slight, flat groove extending one-half distance from periproct to peristome.

*Peristome*.—Slightly anterior, pentagonal, width slightly greater than height in some specimens, less than height in others.

*Floscelle*.—Bourrelets strongly developed; phyllodes long (chart 3,



FIGS. 25-29.—*Pygurus* (*Meipygurus*) *depressus* Agassiz: 25, Apical system of Cotteau's (1869, 31, figs. 1-3) figured specimen from Ranville, France, in the École National Supérieure des mines, Paris,  $\times 15$ . 26, 27, *Astrolampas productus* (Agassiz): 26, Apical system of specimen in the Museum of Comparative Zoology, Harvard, Lower Cretaceous (Neocomian), Mormont és Lasarraz, Switzerland,  $\times 8$ ; 27, phyllode of ambulacrum I of specimen in the Lambert Collection (No. 467), Sorbonne, Paris, from the Lower Cretaceous (Neocomian) at Morteau Doubs), France,  $\times 8$ . 28, *Pseudopygurus letteroni* Lambert: Apical system of specimen from the Jurassic (Sequanian) at Bailly, Yonne, France, in the Lambert Collection, Sorbonne, Paris,  $\times 15$ . 29, *Nucleolites orbicularis* (Phillips): Adoral interambulacral plates in specimen in the Edgwick Museum, Cambridge, England, from the Cornbrash at Scarborough, Yorkshire, England,  $\times 11$ .

fig. a), not broadened in some specimens, slightly broadened in others, with many pore pairs arranged in three series in each half-ambulacrum, in a large specimen (84 mm. long) approximately 18 pore pairs in each outer and inner series, 11 in each median series; pore pairs extending almost to peristome; no buccal pores.

*Tuberculation*.—Tubercles on adoral surface larger than those on adapical surface.

*Occurrence*.—Jurassic (Bathonian-Callovian) of France, Switzerland, England, Madagascar, and British Somaliland.

*Location of type specimen*.—Unknown.

*Remarks*.—There has been considerable controversy over whether or not *P. depressus* and *P. michelini* Cotteau are synonyms. Currie (1925, pp. 66-67) gives a thorough discussion of this problem and concludes that although one may be a variety of the other, they should be considered conspecific.

Lambert and Thiéry (1921, p. 356) considered *P. fungiformis* (Agassiz, L., 1840a, p. 5) the type species of *Mepygurus*, and the senior synonym of *P. michelini*. *P. fungiformis*, however, is a *nomen nudum*.

#### Subgenus PYGUROPSIS De Loriol

*Pyguropsis* De Loriol, 1902. Notes pour servir a l'étude des échinodermes, vol. 10, p. 32. Type species by original designation, *Pygurus noettingi* De Loriol.

*Description*.—The type species of this subgenus differs from all the other species of *Pygurus* in having a thicker test with steeper sides.

*Remarks*.—Mortensen (1948, p. 165) further distinguished this subgenus from *Pygurus* because of its smaller test, broader petals, and periproct on the posterior edge of the test. However, although the holotype is a small specimen, there is no way of knowing that it was an adult since only one specimen is known of this species. The petals are no broader than those in *Pygurus* (*Mepygurus*) *depressus*, and the periproct is in the same position as in *Pygurus lampas*.

*Range and distribution*.—Cretaceous (Cenomanian) of Lebanon. Only one species is known. Fourtau's *Pyguropsis lorioli* is a *Bothryopneustes* as discussed on page 40.

## DESCRIPTION OF TYPE SPECIES

## PYGURUS (PYGUROPSIS) NOETLINGI De Loriol

Plate 4, figures 1-4; chart 3, figure j

*Pygurus noetlingi* De Loriol, 1899. Mém. Soc. Phys. Hist. Nat. Genève, vol. 33, pt. 2, No. 1, p. 4, pl. 1, fig. 3.

*Material*.—Holotype, and only known specimen.

*Shape*.—Small, length slightly greater than width, posterior margin slightly pointed, anterior margin blunted with slight anterior groove; adapical surface inflated, margin very thick with steep sides, greatest height anterior at apical system; adoral surface depressed at peristome, interambulacra inflated.

*Apical system*.—Anterior, four genital pores, tetrabasal.

*Ambulacra*.—Petals very broad, closing distally, equal, petals II, III, and IV extending almost to margin; petals I and V over two-thirds distance to margin. Interporiferous and poriferous zones very wide, tapering distally; pores in each zone widely separated for most of length of zone; pores conjugate, outer pore slitlike, inner pore elongated transversely.

*Periproct*.—Marginal to slightly inframarginal, oval.

*Peristome*.—Anterior, pentagonal, slightly higher than wide.

*Floscelle*.—Bourrelets well developed, inflated; phyllodes well developed, greatly broadened, double pored with three series of pore pairs in each half-ambulacrum: 10 to 12 in the outer series, 3 in the middle, and 2 to 3 in the inner (chart 3, fig. j); interporiferous area very broad; two adjacent pore pairs near peristome, separated from rest of pores, presumably buccal pores.

*Occurrence*.—Cretaceous (Cenomanian), Keft-Akab, Ouadi Sanin, Lebanon.

*Location of type specimen*.—Holotype in De Loriol Collection, Muséum d'Histoire Naturelle, Genève, Switzerland.

*Remarks*.—Lambert (1899, p. 119) suggested from a study of De Loriol's figures that ambulacrum III was different from the others. Ambulacrum III is petaloid like the other petals, but on the holotype the anterior surface is worn, partially obscuring this petal.

The presence of paired buccal pores in this species is most unusual. As discussed on page 7, buccal pores are found in all species having single-pored phyllodes but rarely in species with double-pored phyllodes.



Genus *ASTROLAMPAS* Pomel

*Astrolampas* Pomel, 1883. Class. méth., p. 63. Type species by original designation, *Pygurus productus* L. Agassiz.

## GENERIC DESCRIPTION

Test medium to large, very low, elongate; apical system anterior, tetrabasal; petals long, broad, slightly closed distally, interporiferous zones much wider than poriferous, petaloid pores conjugate, outer pore slitlike, all ambulacral plates double pored; periproct infra-marginal, located three-quarters distance from peristome to posterior margin; peristome anterior, pentagonal; bourrelets slightly developed, not inflated; phyllodes long, narrow, double pored, with two series of pore pairs in each half-ambulacrum; no buccal pores; tubercles adorally slightly larger than adapically.

*Comparison with other genera.*—Mortensen (1948, p. 135) stated that if the apical system of *Astrolampas productus* should be found to be tetrabasal, the genus should be considered a synonym of *Pygurus*. I have studied the apical system of the holotype of *A. productus* and the apical system is tetrabasal, but I do not agree that the genus should be considered a synonym of *Pygurus*. In *A. productus* the bourrelets are not inflated and the phyllodes are narrow with two series of pore pairs, with the inner series widely separated from the outer. In *Pygurus* the bourrelets are strongly inflated, the pore series in a half-ambulacrum in the phyllodes are always close together, and in all the post-Callovian species the phyllodes are greatly widened.

*Astrolampas* is similar to *Pygorhynchus* in petal arrangement and bourrelet development, but differs in having a flatter test, a more anterior periproct, and in general narrower and much longer phyllodes.

*Remarks.*—Lambert and Thiéry (1921, p. 357) refers seven species to this genus, but two of them, Lambert's *Astrolampas romani* and Cotteau's *Botriopygus coquandi*, should be referred to other genera. I studied a toptype specimen of *A. romani* in the U. S. National Museum. Lambert (1904, p. 841) did not figure the adoral surface of his species, but the periproct is too near the posterior margin for an *Astrolampas*, the phyllodes too short and too wide, and the peristome is oblique, not regular. Lambert evidently did not know that the peristome was oblique. In his description he states that in most of the specimens he examined the peristome was covered with matrix, and that it appeared to be pentagonal. If he had known that the peristome was oblique, he certainly would not have



referred it to *Astrolampas*. This species should be referred to *Pygorhynchus*. *B. coquandi* does not have an inframarginal periproct and cannot be an *Astrolampas*. Being Senonian, it probably has single-pored phyllodes and should be referred to *Parapygus*.

*Range and distribution*.—Cretaceous (Valanginian to Cenomanian) of Europe and Syria.

#### DESCRIPTION OF TYPE SPECIES

##### ASTROLAMPAS PRODUCTUS (Agassiz)

Plate 4, figures 5-7; text figures 26, 27

*Pygurus productus* L. Agassiz, 1836a. Mém. Soc. Sci. Nat. Neuchâtel, vol. 1, p. 135.

*Shape*.—Large, holotype 58 mm. long, elongate, slightly pointed posterior, smoothly rounded anterior margin, very low, with greatest height anterior at apical system; adorally depressed with interambulacra slightly inflated.

*Apical system*.—Anterior, tetrabasal (text fig. 26), genital 2 large, extending posteriorly, separating genital plates 4 and 1 but not separating posterior oculars V and I; other genital plates small.

*Ambulacra*.—Petals well developed, broad, equal, lanceolate, extending almost to margin, with slight tendency to close distally; interporiferous zones broad, three times width poriferous zones; poriferous zones wide; outer pore slitlike, inner pore round; pores conjugate.

*Periproct*.—Inframarginal, longitudinal.

*Peristome*.—Anterior, depressed, pentagonal, slightly higher than wide.

*Floscelle*.—Bourrelets slightly developed; phyllodes extremely long, double pored (text fig. 27) with pore pairs arranged in two series in each half-ambulacrum: approximately 15 pore pairs in each outer series, 10 in each inner, with pore pairs arranged longitudinally in inner series, transversely in outer; no buccal pores.

*Tuberculation*.—Tubercles on adoral surface slightly larger than on adapical.

*Occurrence*.—Lower Cretaceous (Neocomian) of France and Switzerland.

*Location of type specimen*.—Museum of Comparative Zoology, Harvard, No. 804.

*Remarks*.—d'Orbigny's (1856, pl. 918, fig. 2) figure of the adoral surface of this species is erroneous in showing inflated bourrelets which project into the peristome, and greatly widened phyllodes.

Genus **PSEUDOPYGURUS** Lambert

*Pseudopygurus* Lambert, 1911b. Ann. Univ. Lyon, ser. 1, vol. 30, p. 184. Type species by monotypy, *Pseudopygurus letteroni* Lambert.

## GENERIC DESCRIPTION

Large, low; apical system tetrabasal; petals II and IV slightly shorter than petals I and V, petal III absent or slightly developed with narrower poriferous zones; all ambulacral plates double pored; peristome regular, longitudinal, pentagonal; periproct inframarginal, longitudinal; bourrelets well developed; phyllodes double pored, with three series of pore pairs in each half-ambulacrum.

*Comparison with other genera.*—*Pseudopygurus* is very similar to *Pygurus* (*Pygurus*). *Pseudopygurus letteroni*, the type species, very closely resembles *Pygurus* (*Pygurus*) *blumenbachi* Kock and Dunker as shown clearly in a comparison of plate 3, figure 4 and plate 5, figure 1. Both species have the same shape, petal arrangement in petals I, II, IV, and V, and similar phyllodes. *P. letteroni* differs only in having a less developed petal III.

*Range and distribution.*—Besides the type species from the Sequanian of France, Petitot (1954) has described a species, *P. ambroggii*, from Oxfordian of Algeria, and Checchia-Rispoli (1941) has figured and described, but not named, another species from the Sequanian of Italian Somaliland.

## DESCRIPTION OF TYPE SPECIES

**PSEUDOPYGURUS LETTERONI** Lambert

Plate 5, figures 1-4; text figure 28

*Pseudopygurus letteroni* Lambert, 1911b. Ann. Univ. Lyon, ser. 1, vol. 30, p. 184 (footnote).

*Material.*—Lambert never figured this species. There are four specimens in the Lambert Collection. The specimen marked type is herein designated the lectotype and is figured in plate 5, figures 1-4. It is well preserved adapically and clearly shows the petals, but adorally the peristome is covered with matrix, and the periproct obscured. A second specimen, also in the Lambert Collection, from a different locality is badly pitted but shows the peristome and periproct.

*Shape.*—Large, low, greatest height anterior at apical system, greatest width posterior of center, anterior margin blunted, posterior pointed, outline roughly pentagonal. Adapically, interambulacrum 5

inflated in ridge along interradial suture, indented along either side at margin. Adorally, all interambulacra inflated relative to ambulacra.

*Apical system*.—Anterior, tetrabasal (text fig. 28).

*Ambulacra*.—Petals II and IV extending two-thirds distance to margin, petals I and V slightly longer, extending over one-half distance to margin. In paired petals, outer pores very elongate transversely, inner pore slightly elongate transversely, pores strongly conjugate, interporiferous zones twice as wide as poriferous, petals closing distally. Petal III (pl. 5, fig. 3) less developed than other petals, with much narrower poriferous zones with interporiferous zones three times as wide as poriferous zones, pores conjugate with outer pore elongate transversely, inner slightly elongated. All petals flush with test.

*Periproct*.—Inframarginal, longitudinal.

*Peristome*.—Anterior, longitudinal, pentagonal, slightly depressed.

*Floscelle*.—Bourrelets well developed, phyllodes broad, double pored, with three series of pore pairs in each half-ambulacrum.

*Occurrence*.—Upper Jurassic (Sequanian), Tonnerre and Baily, Yonne, France.

*Location of type specimen*.—Lambert Collection, Sorbonne, Paris.

*Remarks*.—Checchia-Rispoli (1941) redescribed this genus and species but based his description not on the type specimens, but on specimens from Somaliland which he considered to be conspecific with Lambert's species. However, the Somaliland specimens are quite distinct and should be considered a separate species. The petals in the Somaliland species are longer, extending almost to the margin, and the apical system more central. Maccagno (1947, pp. 132-134, pl. 1, figs. 13, 13a) redescribed the Somaliland specimens, but figured the same specimen that Checchia-Rispoli had figured, but the negative must have been reversed, as the pictures are mirror images of each other.

Lambert stated that ambulacrum III was not petaloid in his species. Although petal III is much narrower than the other petals and its outer pores much less elongated, its pores are much larger than those occurring in the ambulacral plates beyond the petals, and therefore ambulacrum III must be considered as petaloid.

#### Family NUCLEOLITIDAE L. Agassiz and Desor, 1847

Medium to large, circular or elongate; apical system tetrabasal, with or without complementary or catenal plates; petals moderately developed, usually open, narrow with narrow poriferous zones; ambula-

cral plates beyond petals double pored except in *Oolopygus*, phyllodes narrow to slightly widened, with two series of pores in each half-ambulacrum, no buccal pores except in *Oolopygus*; bourrelets moderately developed; adoral tubercles the same size or slightly larger than adapical, no naked granular zone in interambulacrum 5.

*Genera*.—*Nucleolites*, *Pseudosorella*, *Clypeopygus*, *Catopygus*, *Phyllobrissus*, *Pygaulus*, *Pygorhynchus*, *Pygopistes*, *Hypopygurus*, *Plagiochasma*, *Oolopygus*, *Hemicara*.

*Range*.—Jurassic (Bajocian) to Cretaceous (Senonian).

*Comparison with other families*.—The Nucleolitidae are distinguished from the Galeropygidae by their more developed petals, usually more elongate shape, and usually fewer pores in their phyllodes. They are distinguished from the Clypeidae by their narrower petals with narrower poriferous zones, and by the smaller number of pores in their phyllodes. The difference between the two families is not great, for there are some species of *Nucleolites* that have many of the characters of *Clypeus*.

#### Genus NUCLEOLITES Lamarck

*Nucleolites* Lamarck, 1801. *Système des animaux sans vertèbres*, p. 347. Type species by subsequent designation, Lambert, 1808, p. 168, *Nucleolites scutatus* Lamarck.

Synonyms: *Acroniazus* Pomel; *Clitopygus* Pomel; *Chniculus* Pomel; *Echino-brissus* Gray; ? *Heteronucleus* Lambert; *Holcoepygus* Pomel; *Lophopygus* Pomel; *Notopygus* Pomel; *Taphropygus* Pomel; *Thigopygus* Pomel.

#### GENERIC DESCRIPTION

Small to medium size, usually broad with greatest width posterior to center, moderately inflated with thick margins; apical system tetrabasal, with or without complementary or catenal plates; petals long, open, poriferous zones narrowing distally, pores conjugate, outer pore greatly elongated transversely; all ambulacral plates double pored; adorally interambulacrum with single plate (text fig. 29) at peristome preceded by regular series of alternating plates; periproct supramarginal, longitudinal, varying in position from in contact with apical system to widely separated from it, with anal groove extending from apical system or from periproct to posterior margin; peristome anterior, pentagonal, depressed, usually wider than high; bourrelets moderately developed; phyllodes narrow or slightly widened, double pored, with two series of pore pairs in each half-ambulacrum; no buccal pores; tubercles perforate, crenulate, larger adorally than adapically.



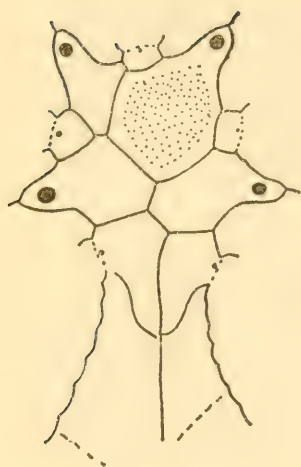
*Comparison with other genera.*—*Nucleolites* is distinguished from *Clypeopygus* by its lower test, and from *Phyllobrissus* by its wider test, less developed bourrelets, and more anterior periproct.

*Remarks.*—The apical system is variable in *Nucleolites*, not only at the generic level but also at the specific. I studied a collection of specimens of *N. scutatus* Lamarck all from the same locality, in which in seven of the specimens the sutures in the apical system were visible. In four of them genital 2 (text fig. 30) was short, not extending far enough posteriorly to separate genital plates 4 and 1, and there were no catenal plates. In one of them (text fig. 31) genital 2 is more elongate posteriorly and separates genital plates 4 and 1, and in one of them there are numerous catenal plates (text fig. 32) joining the posterior ocular plates to the periproct. Although no complementary plates occurred in any of the seven specimens, both Cotteau (1872, Pal. franc., Jur., pl. 77, fig. 5) and Beurlen (1933, p. 58) found them in other specimens. In some species there are specimens with many complementary plates as in *N. orbicularis* (Phillips) (text fig. 33) and *N. major* (Agassiz) (text fig. 34), few as in a specimen of *N. burgundiae* (Cotteau) (text fig. 36), and none as in a specimen of *N. hugi* (Agassiz) (text fig. 35). Genital 2 is often small, not extending posteriorly between genital plates 4 and 1, as in a specimen of *N. scutatus* (text fig. 30), or very large, extending not only between the posterior genital plates but also between oculars V and I, as in a specimen of *N. brodici* (Wright) (text fig. 37).

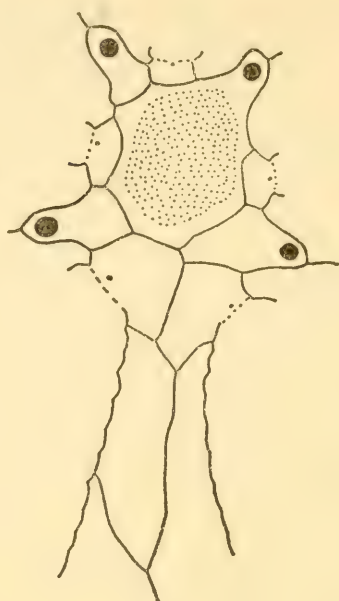
The phyllodes, on the other hand are remarkably consistent within the genus. There are always two series of pore pairs in each half-ambulacrum, usually with approximately 10 in each outer series and 4 to 6 in each inner, as in *N. gracilis* (Agassiz) (text fig. 38), *N. placentula* (Desor) (text fig. 39), *N. lorioli* (Cotteau) (text fig. 40), *N. rotundus* (Peron and Gauthier) (text fig. 41), *N. amplus* Agassiz (text fig. 42), *N. orbicularis* (Phillips) (text fig. 43), *N. burgundiae* (Cotteau) (text fig. 44), *N. major* (Agassiz) (text fig. 45), *N. clongatus* Agassiz (text fig. 46), *N. scutatus* Lamarck (text fig. 49), and *N. subquadratus* Agassiz (text fig. 48). In *N. hugi* (Agassiz) (text fig. 47) the phyllodes are similar except that they are longer, having approximately 18 pore pairs in each outer series and 6 to 8 in each inner.

Desor's *Echinobrissus placentula* from the Aptian is a *Nucleolites* and not a *Nucleopygus* as determined by Lanibert and Thiéry (1921, p. 347). The phyllodes (text fig. 39) are double pored on a specimen

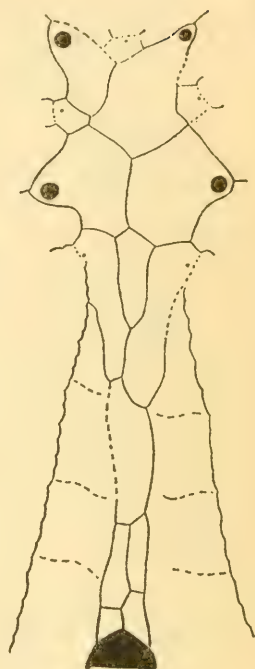




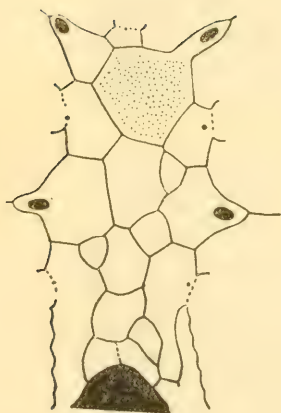
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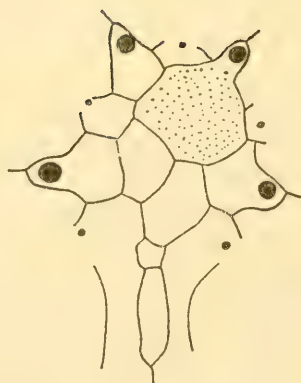
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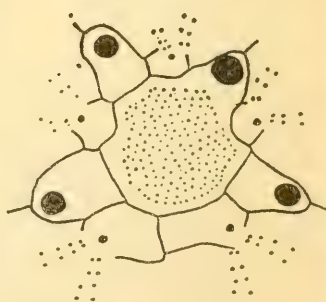
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FIGS. 30-35.—Apical systems in species of *Nucleolites* showing the variation within a species and between species: 30-32, *Nucleolites scutatus* Lamarck from the Upper Jurassic (Oxfordian) at Villers, France: 30, Showing genital 2 not extending posteriorly between genitals 1 and 4 and no catenal plates, USNM 131280a; 31, showing genital 2 separating plates 4 and 1, with no catenal plates, USNM 19546a; 32, showing many catenal plates, USNM 195466. 33, *Nucleolites orbicularis* (Phillips) with many complementary plates, from Jurassic (Cornbrash) at Scarborough, Yorkshire, England, in Sedgwick Museum (J18148), Cambridge, England. 34, *Nucleolites major* (Agassiz) from Toul, France, in the École Nationale Supérieure des Mines, Paris. 35, *Nucleolites hugi* (Agassiz) from specimen in Muséum National d'Histoire Naturelle, Paris, no locality. All figures  $\times 15$ .

studied in the Muséum d'Histoire Naturelle, Genève, Switzerland, not single pored as typical in *Nucleopygus*.

*Range and distribution.*—Middle Jurassic (Bajocian) to Cretaceous (Cenomanian) of Europe and North Africa. Lambert and Thiéry (1921, pp. 343-346) refer many Cenomanian and post-Cenomanian species to *Nucleolites*, *Echinobrissus* (an objective synonym of *Nucleolites*), and *Clitopygus* (herein considered a subjective synonym of *Nucleolites*). Most of these species and probably all the post-Cenomanian species belong to other genera. Among these species, Fourtau's *Echinobrissus ammonis* and *E. lefebvrei* from the Turonian have single-pored phyllodes and broad petals and are herein referred to *Petalobrissus* (see p. 123 for a redescription of these two species). Clark's *Echinobrissus expansus* according to Cooke (1953, p. 13) is based on a specimen of *Nucleolites scutatus* from the Jurassic of Europe. Lambert's *Clitopygus marticensis* from the Santonian has single-pored phyllodes and probably should be referred to *Rhynchopygus*. The phyllodes have never been figured in any of the other post-Cenomanian species that Lambert and Thiéry refer to *Clitopygus*, but it is probable that they are all single pored and that the species should be referred to other genera. Ikins' (1940, p. 28) *Nucleolites wilderac* from the Senonian is, according to Cooke (1953, p. 17), conspecific with the Texan specimens of Weisbord's (1934, p. 191) *Echinobrissus cubensis*, which is herein (p. 122) considered a *Petalobrissus*.

I have seen specimens of Peron and Gauthier's *Echinobrissus rotundus* in the Lambert Collection and include a photograph of one of them (pl. 7, fig. 7). It has double-pored phyllodes (text fig. 41) and is the latest occurring *Nucleolites* (Cenomanian) that I have seen.

#### DESCRIPTION OF TYPE SPECIES

##### NUCLEOLITES SCUTATUS Lamarck

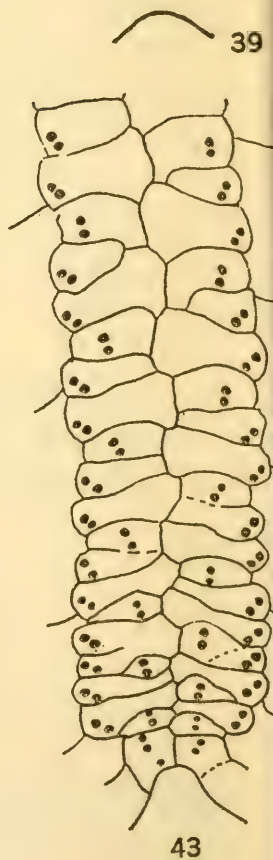
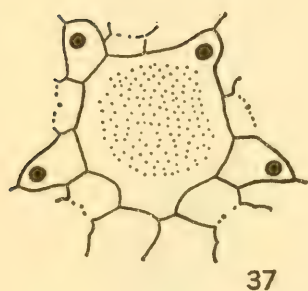
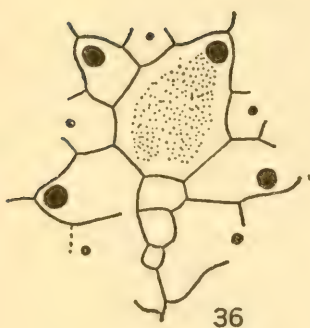
Plate 6, figures 1-3; text figures 30-32, 49

*Nucleolites scutatus* Lamarck, 1816. Animaux sans vertèbres, vol. 3, p. 36.

*Material.*—Fifty specimens studied in the U. S. National Museum.

*Shape.*—Small to medium size, subquadrangular in marginal outline, expanding posteriorly, with greatest width posterior to center, anterior margin smoothly rounded, posterior indented at anal groove; adapically inflated, with thick margins, sides sloping steeply; adorally pulvinate with ambulacra slightly depressed, peristome very depressed.

*Apical system.*—Anterior, tetrabasal (text figs. 30-32), genital 2



(See legend on opposite page.)

large usually extending posteriorly only to genital plates 4 and 1, but in some specimens (text fig. 31) extending more posteriorly, separating these genitals; oculars V and I large, in some specimens short (text fig. 30), in others long, extending posteriorly (text fig. 32); catenal plates extending from posterior oculars to periproct present (text fig. 32) in few specimens, but usually absent; no complementary plates on any specimens studied by this author, but Cotteau (1872, Pal. franc., Jur., pl. 77, fig. 5) and Beurlen (1933, p. 58) show one in their figures.

*Ambulacra*.—Petals well developed, open, equal length, extending two-thirds distance to margin, flush with test; interporiferous zones almost twice width of poriferous zones; poriferous zones narrowing distally, pores conjugate, outer pore transversely elongate, inner circular.

*Periproct*.—Supramarginal, between one-third and one-half distance from apical system to posterior margin; longitudinal, slight groove from apical system to periproct, deep groove from periproct to posterior margin, groove continuing to adoral surface.

*Peristome*.—Anterior, depressed, pentagonal, wider than high.

*Floscelle*.—Bourrelets slightly developed; phyllodes double pored, arranged in two series in each half-ambulacrum, approximately 10 pore pairs in each outer series, 4 to 6 in each inner (text fig. 49).

*Tuberculation*.—Tubercles perforate, crenulate, larger adorally than adapically.

*Occurrence*.—Upper Jurassic (Oxfordian-Rauracian) of England, France, and Switzerland.

*Location of type specimen*.—Unknown.

FIGS. 36-43.—36, *Nucleolites burgundiae* (Cotteau): Apical system showing few complementary plates on specimen in Museum of Comparative Zoology, Harvard, from Jurassic (Bathonian) at Selongey (Côte-d'Or), France,  $\times 12$ . 37, *Nucleolites brodiei* (Wright): Apical system with large genital 2 separating posterior oculars, from specimen in Muséum National d'Histoire Naturelle, Paris, Jurassic (Portlandian), St. Saire, France,  $\times 15$ . 38, *Nucleolites gracilis* Agassiz: Phyllode of ambulacrum V of holotype in Museum of Comparative Zoology, Harvard, from the Jurassic (Upper Oxfordian) at Raedersdorf Haute, Switzerland,  $\times 10$ . 39, *Nucleolites placentula* (Desor): Phyllode of specimen from De Liori Collection, Muséum d'Histoire Naturelle, Genève, Switzerland, from the Lower Cretaceous (Aptian) at La Presta (Neuchâtel), Switzerland,  $\times 15$ . 40, *Nucleolites lorioli* (Cotteau): Phyllode of specimen in Muséum National d'Histoire Naturelle, Paris, from the Middle Jurassic (Bajocian) at St. Michiel, France,  $\times 15$ . 41, *Nucleolites rotundus* (Peron and Gauthier): Phyllode of ambulacrum I of specimen in Lambert Collection (No. 253), Sorbonne, Paris, from the Cretaceous (Cenomanian) at Bou Saada, Algeria,  $\times 10$ . 42, *Nucleolites amplius* Agassiz: Phyllode of ambulacrum II of specimen in Naturhistorisches Museum (No. M1521/1), Basel, Switzerland, from Middle Jurassic (Bathonian), Discoideen-Schichten, Aargauer, Jura, Herznach, Switzerland,  $\times 15$ . 43, *Nucleolites orbicularis* (Phillips): Phyllode of ambulacrum IV of specimen J18145 in Sedgwick Museum, Cambridge, England, from Scarborough, Yorkshire, England,  $\times 10$ .





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FIGS. 44-49.—44, *Nucleolites burgundiae* (Cotteau): Phyllode of specimen in Museum of Comparative Zoology, Harvard, from Jurassic (Bathonian) at Selongey (Côte-d'Or), France,  $\times 10$ . 45, *Nucleolites major* (Agassiz): Phyllode of ambulacrum I of specimen in École Nationale Supérieure des Mines, Paris, from Toul, France,  $\times 10$ . 46, *Nucleolites elongatus* Agassiz: Phyllode of ambulacrum III of specimen in Muséum National d'Histoire Naturelle, Paris, no locality data,  $\times 15$ . 47, *Nucleolites hugi* (Agassiz): Phyllode of ambulacrum V from specimen in Lambert Collection, Sorbonne, Paris, no locality data,  $\times 10$ . 48, *Nucleolites subquadratus* Agassiz: Phyllode of ambulacrum V of specimen in Museum of Comparative Zoology, Harvard (No. 965), from the Lower Cretaceous (Neocomian) at Mieger et Billecul (Jura), Switzerland,  $\times 10$ . 49, *Nucleolites scutatus* Lamarck: Phyllode of ambulacrum I of specimen USNM 19546, from the Upper Jurassic (Oxfordian) at Villers, France,  $\times 10$ .



## Synonyms of NUCLEOLITES

*Echinobrissus* Gray, 1825. Ann. Philos., p. 429. Type species, *Nucleolites scutatus* Lamarck, by subsequent designation, Cooke, 1946, p. 222.

*Remarks.*—There has been considerable confusion between *Echinobrissus* and *Nucleolites*. Most authors (e.g., Mortensen, Lambert and Thiéry, Duncan, and Cotteau) have used the name *Echinobrissus* even though they attributed it to a pre-Linnaean author, Breynius, 1732. They considered *Nucleolites clunicularis* Phillips the type species. Since *N. clunicularis* was not included among the two species that Gray referred to his *Echinobrissus*, it cannot be the type species. Cooke's designation of *N. scutatus* as the type species is correct, making *Echinobrissus* a junior objective synonym of *Nucleolites*. Even if *N. clunicularis* were the type species of *Echinobrissus*, this genus could not stand. *N. clunicularis* is very similar to *N. scutatus* and certainly congeneric, the two species being distinguished from each other only by a slight difference in shape of their test, and in the length of their anal groove.

*Acromazus* Pomel, 1883. Class méth., p. 58. Type species herein designated, *Echinobrissus burgundiae* (text figs. 36, 44) Cotteau, 1871, Pal. franc., Jur.

One of the specimens figured herein was among the four specimens labeled "types" in the Cotteau Collection at the École National Supérieure des Mines, Paris.

*Clitopygus* Pomel, 1883. Op. cit., p. 58. Type species *Echinobrissus lorioli* (text fig. 40) Cotteau, 1871, Pal. franc., Jur., by subsequent designation, Lambert (1898, p. 468).

*Chniculus* Pomel, 1883. Op. cit., p. 57. Type species herein designated, *Nucleolites gracilis* (pl. 6, figs. 5, 6; text fig. 38) L. Agassiz, 1840b.

I found the holotype of this species in the Museum of Comparative Zoology, Harvard. Its location has been unknown for many years.

*Holcoopygus* Pomel, 1883. Op. cit., p. 58. Type species herein designated, *Nucleolites elongatus* (pl. 6, fig. 7; text fig. 46) L. Agassiz, 1840b.

*Lophopygus* Pomel, 1883. Op. cit., p. 57. Type species by monotypy, *Nucleolites cordatus* Goldfuss, 1826.

*Notopygus* Pomel, 1883. Op. cit., p. 58. Type species herein designated, *Nucleolites amplus* (pl. 6, fig. 8, text fig. 42) L. Agassiz, in Agassiz and Desor (1847).

*Taphropygus* Pomel, 1883. Op. cit., p. 59. Type species herein designated *Nucleolites subquadratus* (pl. 6, fig. 9; text fig. 48) L. Agassiz, 1839. Both Lambert and Thiéry (1921, p. 348) and Mortensen (1948, p. 146) considered *Taphropygus* a synonym of *Clypeopygus*, but the test in *N. subquadratus* is too inflated and the petals too narrow for *Clypeopygus*.

*Thigopygus* Pomel, 1833. Op. cit., p. 59. Type species herein designated, *Echino-brissus humilis* Gauthier.

*Remarks.*—Most authors have considered the above genera of Pomel's as synonyms of *Nucleolites*. They are distinguished from each other and *Nucleolites* on slight differences in shape, position of the periproct, and length of the anal groove. These differences are often variable within a single species and certainly are not of generic importance. The phyllodes and petals are very similar in all these "genera." I have seen specimens of all the type species except *Thigopygus*, but do not believe that a redescription of these species is justified since they are all so similar to each other. However, since photographs have never been published of most of these species, nor drawings of their phyllodes, I have included them herein.

#### ? Synonym of **NUCLEOLITES**

*Heteronucleus* Lambert, 1911b. Ann. Univ. Lyon, ser. I, vol. 30, p. 184. Type species by original designation, *Heteronucleus peroni* Lambert.

*Remarks.*—Lambert erected this genus because he thought that ambulacrum III was not petaloid in the type species. In all other respects, he considered it similar to *Clitopygus* (herein considered a synonym of *Nucleolites*). In his brief description of the holotype, and only specimen of this species, he stated that the pores were microscopic in ambulacrum III. I have studied this specimen and have found that ambulacrum III was petaloid originally, but owing to the poor preservation of the anterior area of the holotype, most of this petal is missing. Three plates are present near the apical system in ambulacrum III, and their pores are just as large as those in the other petals. Since Lambert's description is very brief, and the species has never been figured, I include below a description and illustrations of the holotype. According to Lambert, the holotype is from the Senonian, but I suspect from the worn appearance of the specimen and the many primitive features that ally it with *Nucleolites*, that it is reworked from older strata.

#### DESCRIPTION OF TYPE SPECIES

#### **HETERONUCLEUS PERONI** Lambert

Plate 44, figures 9-12

*Heteronucleus peroni* Lambert, op. cit., p. 184 (footnote).

*Material.*—Only one specimen, the holotype, is known. This specimen is finely fractured with the test broken or worn away in many

places, particularly marginally and in the right anterior portion of the adapical surface. The peristome is covered with matrix.

*Shape*.—Small, holotype only 19 mm. long, probably an immature specimen, oblong, low, with greatest height anterior to center.

*Apical system*.—Anterior, tetrabasal, oculars large, posterior oculars in contact with each other; madreporite large; four genital pores.

*Ambulacra*.—Petals broad, open, approximately equal in length, petals II, III, and IV extending almost to margin, petals I and V extending two-thirds distance to margin. Interporiferous zones broad, almost twice width of poriferous zones. Pores conjugate, outer pore slitlike, inner round or slightly elongated transversely.

*Periproct*.—Supramarginal, approximately two-thirds distance from apical system to posterior margin, longitudinal, in slight groove.

*Peristome*.—Covered with matrix.

*Floscelle*.—Covered with matrix but phyllodes probably double pored as typical in *Nucleolites*.

*Occurrence*.—? Upper Cretaceous (Senonian) at Djelfa, Algeria.

*Location of type specimen*.—Holotype in Lambert Collection at the Sorbonne, Paris.

#### Genus PSEUDOSORELLA Etallon

*Pseudosorella* Etallon, 1859. Mem. Soc. Emulation de Montbéliard, vol. 3, (1858), pp. 415-416. Type species by monotypy, *Desoria orbignyana* Cotteau. Cotteau (1862) and all subsequent authors have used the spelling "Pseudodesorella" for this genus. Etallon's spelling of the word is evidently not a typographic error since he spells it *Pseudosorella* in both instances in which the name is used. He combined "pseudo" and "desorella" and presumably dropped the "de" for simplicity. This original spelling must be used.

Synonym: *Neoclypeus* De Loriol.

#### GENERIC DESCRIPTION

Medium to large, broad, inflated, with rounded margin, adorally ambulacra depressed; apical system central to slightly anterior, tetrabasal; petals broad, long, extending almost to margin, with wide interporiferous zones, narrow poriferous zones, open or with slight tendency to close distally, pores conjugate, outer pore elongated into slit, inner round; all ambulacral plates double pored; periproct supramarginal, in contact with apical system, in deep groove extending from apical system to margin; peristome central or slightly anterior, pentagonal, wider than high; bourrelets present; phyllodes well developed, slightly broadened, double pored, with many pore pairs in two series in each half-ambulacrum; no buccal pores.



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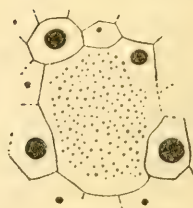
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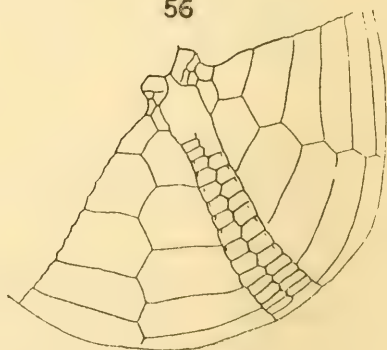
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(See legend on opposite page.)



*Comparison with other genera.*—*Pseudosorella* is very distinct from any other genus. Its phyllodes and position of periproct are similar to those of *Nuculolites*, but its shape and its petals easily distinguish it. Its periproct is similar to *Clypeus*, but its petals are very different, having very narrow poriferous zones, and its test is much higher.

*Range and distribution.*—Jurassic (Rauracian) of France, Switzerland, and Syria. The age of the Syrian species is not certain but is presumed to be Rauracian.

#### DESCRIPTION OF TYPE SPECIES

##### PSEUDOSORELLA ORBIGNYANA (Cotteau)

Plate 9, figure 13; plate 10, figures 1, 2; text figure 50

*Desoria orbignyana* Cotteau, 1855. Éch. foss., L'Yonne, vol. 1, p. 227, pl. 33, figs. 9-11.

*Material.*—One specimen studied in the Muséum National d'Histoire Naturelle and a second in the École National Supérieure des Mines in Paris. This latter specimen is Cotteau's (1872, pl. 84, Pal. franc., Jur.) figured specimen.

*Shape.*—Medium size, very broad, inflated with rounded margin, greatest height posterior to center; adorally, ambulacra depressed, interambulacra inflated.

*Apical system.*—Central, tetrabasal.

*Ambulacra.*—Petals broad, long, almost extending to ambitus; open; paired petals straight or with distal portions slightly curved posteriorly; interporiferous zones very wide, poriferous zones narrow; with width of poriferous zones decreasing distally; pores strongly conjugate, outer pore slitlike, inner pore round.

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FIGS. 50-57.—50, *Pseudosorella orbignyana* (Cotteau): Phyllode of ambulacrum II from specimen in Muséum National d'Histoire Naturelle, Paris, from the Corallian at Valfin (Jura), France,  $\times 7$ . 51, *Pseudosorella syriaca* (De Loriol): Phyllode from ambulacrum V of lectotype in Muséum d'Histoire Naturelle, Genève, Switzerland, from the Jurassic at Mar-Abda at the bottom of the Ghazir Valley, Syria,  $\times 15$ . 52, *Clypeopygus paultrai* (Cotteau): Phyllode of ambulacrum II of specimen in Lambert Collection, Sorbonne, Paris, from the Lower Cretaceous (Neocomian), at Marolles,  $\times 10$ . 53, *Catopygus fenestratus* Agassiz: Phyllode of ambulacrum I of USNM 131271, from Upper Cretaceous (Maestrichtian) at Ciply (near Mons), Lienard Quarry, Belgium,  $\times 15$ . 54, *Catopygus mississippiensis* Cooke: Phyllode of ambulacrum I of holotype, USNM 108379, from Upper Cretaceous (Maestrichtian), from bed of a branch stream near Mobile and Ohio Railroad tracks about 5 miles northeast of Houston, Miss. 55-57, *Catopygus carinatus* (Goldfuss): 55, Phyllode of ambulacrum V of USNM 131277, from the Cretaceous (Cenomanian) at Saint Didier des Bois (Eure), France,  $\times 15$ ; 56, apical system of same specimen,  $\times 20$ ; 57, adoral view of interambulacra 4, 5, showing plate arrangement of same,  $\times 3$ .



*Periproct*.—Supramarginal, in contact with apical system, elongate longitudinally, in deep groove extending from apical system to margin.

*Peristome*.—Central or slightly anterior of center, wider than high, pentagonal.

*Floscelle*.—Bourrelets present; phyllodes well developed, slightly broadened, long, double pored (text fig. 50), with approximately 15 pore pairs in each outer series, 8 to 10 in inner series; no buccal pores.

*Tuberculation*.—Adorally tubercles approximately same as adapically.

*Occurrence*.—Jurassic (Rauracian) at Andryes, Mery-sur-Yonne; Saint-Martin sur Armancon. Yonne, and Valfin, Jura, France.

*Location of type specimen*.—Not known.

#### Synonym of PSEUDOSORELLA

*Neoclypeus* De Loriol, 1901. Notes pour servir à l'étude des échinodermes, vol. 9, pp. 33-34. Type species by monotypy, *Neoclypeus syriacus* de Loriol.

#### DESCRIPTION OF TYPE SPECIES

#### PSEUDOSORELLA SYRIACA (De Loriol)

Plate 10, figures 3-4; text figure 51

*Neoclypeus syriacus* De Loriol, op. cit., pp. 34, 35, pl. 2, fig. 27.

*Material*.—There are two specimens of this species in the De Loriol Collection. One of them, the specimen figured by De Loriol, is herein designated as the lectotype and figured on my plate 10, figures 3, 4. Although fractured, this specimen and the second specimen show most of the features of the species except for the apical system.

*Shape*.—Medium size, broad, margin rounded, of medium height; adorally, ambulacra depressed, interambulacra slightly inflated.

*Apical system*.—Central, or slightly anterior, further details not visible, but from age presumably tetrabasal.

*Ambulacra*.—Petals broad, straight, long, extending almost to margin, open, with slight tendency to close distally; interporiferous zones very wide, poriferous zones narrow, with width of poriferous zones decreasing distally; pores strongly conjugate, outer pore slit-like, inner pore round.

*Periproct*.—Supramarginal, in contact with apical system, elongate longitudinally, in deep groove extending from apical system to margin.

*Peristome*.—Slightly anterior, pentagonal, wider than high.

*Floscelle*.—Bourrelets present; phyllodes slightly broadened, double pored, with 8 to 10 pore pairs in each outer series, 5 to 7 in each inner series in each half-ambulacrum (text fig. 51); no buccal pores.

*Occurrence*.—Jurassic, Mar-Abda, at the bottom of the Ghazir Valley, Syria. De Loriol considered this species Cenomanian because of its association with radioles he thought to be of that age. According to Lambert and Thiéry (1921, p. 343, footnote) these radioles were misidentified, and all the other species described by De Loriol from Mar-Abda belong to genera essentially Jurassic.

*Location of type species*.—The lectotype and one paratype are in the De Loriol Collection at the Muséum d'Histoire Naturelle at Genève, Switzerland.

*Remarks*.—Lambert and Thiéry (1921, p. 343) and Mortensen (1948, p. 131) considered *Neoclypeus* a synonym of *Pseudosorella*. Its type species is very similar to the type species of *Pseudosorella* and certainly congeneric with it. Both have broad tests, with long petals, conjugate pores, periproct in contact with the apical system and in a deep groove extending to the margin. Their floscelles are very similar, with bourrelets, and with phyllodes with two series of pore pairs in each half-ambulacrum.

De Loriol states that the pores in the phyllodes are arranged in two simple series. Mortensen (1948, p. 132) quoted this statement and suggested that in this character *P. syrica* recalls *Galeroclypeus*. However, the phyllodes are well developed in *P. syrica*, with many pore pairs arranged in two series in each half-ambulacrum, whereas there are no phyllodes in *Galeroclypeus*.

#### Genus CLYPEOPYGUS d'Orbigny

*Clypeopygus* d'Orbigny, 1856. Pal. franc., Crétacé, vol. 6, p. 201. Type species, *Clypeus paultrai* Cotteau by subsequent designation, d'Orbigny, 1858, op. cit., p. 422.

#### GENERIC DESCRIPTION

Medium size, elongate, flat, greatest width posterior to center, adapical surface flattened, adoral depressed; apical system tetrabasal, anterior; petals equal, broad, open, outer pore elongated transversely, all ambulacral plates double pored; periproct supramarginal, with deep triangular groove extending from periproct to posterior margin; peristome anterior, pentagonal, width equal to height; bourrelets well

developed, phyllodes double pored, broad, with two series of pore pairs in each half-ambulacrum; no buccal pores.

*Comparison with other genera.*—Duncan (1891, p. 188) considered *Clypeopygus* as only a subgenus of *Clypeus*, differing from it in having a more anteriorly eccentric apical system, and narrower poriferous zones. However, *Clypeopygus* is a more advanced form than *Clypeus* and certainly not a subgenus of it. The phyllodes of *Clypeopygus* are broad with only two series of pore pairs with few pore pairs in each, as opposed to the long, not widened phyllodes of *Clypeus* with three series of pore pairs in each half-ambulacrum. Furthermore, the peristome in *Clypeopygus* is very eccentric anteriorly, whereas in *Clypeus* it is central or only slightly anterior.

Lambert and Thiéry (1921, p. 349) consider *Petalobrissus* a subgenus of *Clypeopygus*. As *Clypeopygus* has double pores in its phyllodes and no buccal pores, it must be considered generically distinct from the more advanced *Petalobrissus* which has single pores in its phyllodes and buccal pores. Lambert and Thiéry were not aware of these differences. In addition to these differences, *Clypeopygus* is much more depressed than *Petalobrissus*.

*Clypeopygus* is most similar to *Nucleolites*, both genera having similar petals, phyllodes, and periproct. They differ only in that the test is more depressed in *Clypeopygus*.

Lambert and Thiéry refer many species to this genus. As I have discussed on page 120, few of the post-Cenomanian species, perhaps none of them, belong to this genus. Among the pre-Cenomanian and Cenomanian species, Clark's *Echinobrissus angustatus* has single-pored phyllodes with very few pores, buccal pores, slightly developed phyllodes, and a high test, and is herein referred to *Nucleopygus* (see p. 167). *Nucleolites subquadratus* Agassiz is too inflated for *Clypeopygus*, and should be referred to *Nucleolites* (see p. 63).

Weisbord (1934, p. 32) provisionally referred an Upper Cretaceous species to *Clypeopygus*, *C. habanensis*. I believe, however, that this species should be referred to *Hardouinia*. I have studied his holotype and found single-pored phyllodes. The shape of the test, and location and shape of the periproct is very similar to *Hardouinia*. Of even greater significance, its genital plates are greatly elongated, extending between the petals, a character typical in *Hardouinia*.

*Range and distribution.*—Cretaceous (Neocomian-Cenomanian) of Europe and Africa.

## DESCRIPTION OF TYPE SPECIES

**CLYPEOPYGUS PAULTREI** (Cotteau)

Plate 13, figure 9; text figure 52

*Clypeus paultrei* Cotteau, 1851. Bull. Soc. Sci. Hist. Nat. Yonne, vol. 5, p. 291.

*Material*.—I was able to find only one specimen of this species in Europe, and that one was in the Lambert Collection at the Sorbonne, Paris. Unfortunately, this specimen is not well preserved.

*Shape*.—Medium size (Cotteau's, 1859, pl. 57, figs. 8-11, figured specimen 55 mm. long), very depressed with adapical surface flattened, adoral depressed; marginal outline elongate, slight anterior notch, greatest width posterior to center.

*Apical system*.—Anterior, tetrabasal, posterior genital plates not in contact, separated by genital 2.

*Ambulacra*.—Petals broad, equal, flush, straight, open or with very slight tendency to close distally. Poriferous zones tapering distally, pores conjugate, outer pore elongated transversely, slitlike; inner pore round.

*Periproct*.—Supramarginal, in triangular notch with flat floor extending to posterior margin; periproct opening between one-half and two-thirds distance from apical system to posterior margin.

*Peristome*.—Anterior, pentagonal, width equal to height, depressed.

*Floscelle*.—Bourrelets strongly developed, inflated; phyllodes broad, double pored (text fig. 52), with pore pairs arranged in two series in each half-ambulacrum, looplike in arrangement, approximately 10 pore pairs in each outer series, 5 in each inner; no buccal pores.

*Occurrence*.—Lower Cretaceous (Neocomian), Saint-Sauveur, Marolles, Yonne, France.

*Location of type specimen*.—According to Cotteau (1859, p. 94), the type specimen was in his collection in the École des Mines, Paris.

**Genus CATOPYGUS** L. Agassiz

*Catopygus* L. Agassiz, 1836b. Prod. monogr. radiaires, p. 185. Type species by subsequent designation, Cotteau, 1869, Pal. franc., Jur., p. 121, *Nucleolites carinatus* Goldfuss, 1826.

Synonym: *Penesticta* Pomel.

## GENERIC DESCRIPTION

Small, oval, highly inflated adapically, usually with slightly pointed posterior margin; flat or slightly convex adorally; apical system



anterior, tetrabasal, three or four genital pores; petals equal, flush, open or slightly closing distally, pores usually conjugate, all ambulacral plates double pored; periproct marginal, longitudinal, not visible dorsally; peristome anterior, higher than wide, pentagonal; bourrelets well developed, phyllodes broad, double pored, with pore pairs in two series in each half-ambulacrum, inner or lower pore of a pore pair usually smaller than other pore; no buccal pores.

*Comparison with other genera.*—*Catopygus* is very similar to *Phyllobrissus* (see p. 76 for discussion of their similarities and differences). It strongly resembles *Pygaulus* in shape, petal arrangement, and position and shape of periproct, but differs in having a pentagonal peristome and a well-developed floscelle with wide phyllodes and well-developed bourrelets.

*Remarks.*—As the phyllodes have been illustrated in very few species of this genus, I include a drawing of the phyllodes of *Catopygus fenestratus* Agassiz (text fig. 53) and *Catopygus mississippiensis* Cooke (text fig. 54).

*Range and distribution.*—Jurassic to Cretaceous (Kimmeridgian to Senonian) of worldwide distribution. Lambert and Thiéry (1921, p. 353) list two post-Mesozoic species: *Catopygus recens* A. Agassiz, and *Catopygus cajonensis* Kew. I have studied the type specimens of both Kew's *C. californicus* and *C. cajonensis*. They are both internal molds, and from their shape and the anterior location of their peristomes, they appear to be spatangoids and certainly not *Catopygus*. Kew referred both species only provisionally to *Catopygus*. *Catopygus recens* is a *Studeria*.

#### DESCRIPTION OF TYPE SPECIES

##### CATOPYGUS CARINATUS (Goldfuss)

Plate 10, figures 5-8; text figures 55-57

*Nucleolites carinatus* Goldfuss, 1826. *Petrefacta Germaniae*, p. 142, pl. 43, fig. 11.

*Material.*—Over 60 specimens studied in the U. S. National Museum.

*Shape.*—Small, elongate, inflated, with posterior margin pointed at periproct, greatest height at apical system or slightly posterior to it, greatest width posterior to center; adoral surface flattened or slightly convex.

*Apical system.*—Anterior, tetrabasal (text fig. 56), four genital pores, pore of genital 3 at greater distance from other pores; posterior genital plates not in contact, separated by genital 2.



*Ambulacra*.—Petals broad, flush, extending over two-thirds distance to margin; open or with slight tendency to close. Interporiferous zones twice width poriferous zones; poriferous zones narrow, tapering distally; pores conjugate, outer pore elongated transversely, inner round.

*Adoral interambulacra*.—Plate arrangement of interambulacrum 5 similar to other areas (text fig. 57), single plate at peristome, preceded by alternating plates.

*Periproct*.—High on margin, surrounding area slightly inflated, opening longitudinal, not visible dorsally.

*Peristome*.—Anterior, pentagonal, higher than wide, flush with test.

*Floscelle*.—Bourrelets well developed, inflated with steep vertical sides, phyllodes broadened (text fig. 55), double pored, outer pore more than twice size of inner pore; 10 to 11 pore pairs in each outer series, 4 to 5 in each inner series; no buccal pores.

*Tuberculation*.—Adoral tubercles same size as adapical.

*Occurrence*.—Cenomanian of France and Germany.

*Location of type specimen*.—Not known.

#### Synonym of CATOPYGUS

*Penesticta* Pomel, 1883. Class. méth., p. 64. Type species by monotypy, *Oolopygus bargesii* d'Orbigny, 1856.

#### DESCRIPTION OF TYPE SPECIES

##### CATOPYGUS BARGESII (d'Orbigny)

Plate 11, figures 1-3; text figures 58, 59

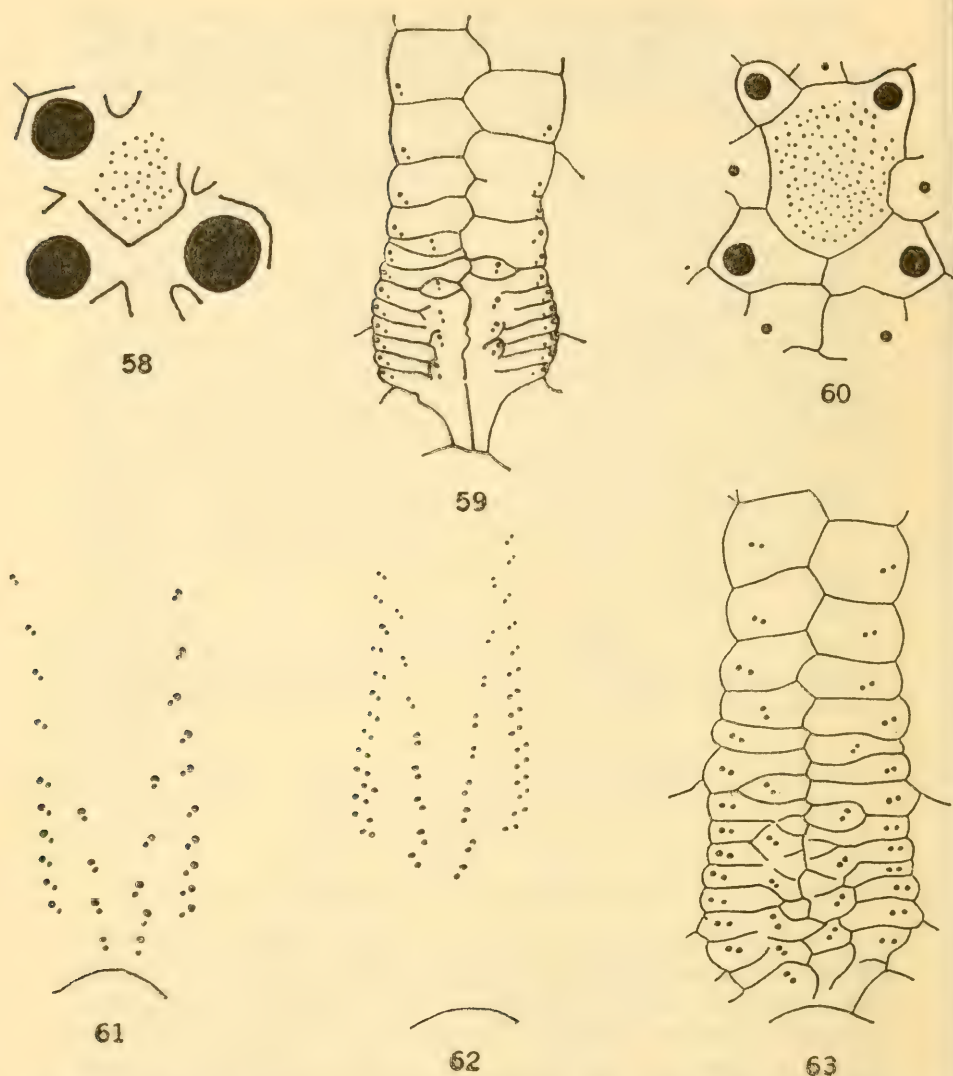
*Oolopygus bargesii* d'Orbigny, 1856. Pal. franc., Crétacé, vol. 6, atlas, pl. 976.

*Material*.—Two specimens were seen in the d'Orbigny Collection, Muséum National d'Histoire Naturelle, Paris; two in the Lambert Collection at the Sorbonne, Paris, and three in the De Loriol Collection in the Muséum d'Histoire, Naturelle, Genève, Switzerland. All these specimens were topotypic. None of the specimens are well preserved, being badly weathered or partially covered with matrix.

*Shape*.—Small, approximately 25 mm. long, elongate with greatest width posterior to center, highly inflated with greatest height posterior to center, steep sides; adoral surface flattened.

*Apical system*.—Anterior, tetrabasal, three genital pores, no pore in genital 2 (text fig. 58); posterior genital plates in contact with each other.

*Ambulacra*.—Petals slightly developed, pores in petals small, only



FIGS. 58-63.—58, 59, *Catopygus bargesi* (d'Orbigny): 58, Apical system, partially preserved with genital pores greatly enlarged by weathering from specimen in the Muséum National d'Histoire Naturelle, Paris, from the Cretaceous (Cenomanian) at Cassis, France,  $\times 20$ ; 59, phyllode of ambulacrum V of specimen in Lambert Collection, Sorbonne, Paris, from the Cretaceous (Cenomanian) at La Badoule, France,  $\times 15$ . 60, 61, *Phyllobrissus gresslyi* (Agassiz): 60, Apical system of USNM 131275, from the Lower Cretaceous (Neocomian), at Auxerre (Yonne), France,  $\times 15$ ; 61, phyllode of ambulacrum IV of same specimen,  $\times 15$ . 62, *Phyllobrissus cerceleti* (Desor): Phyllode of ambulacrum II of Lambert's (1892, pl. 4, fig. 18) figured specimen in the Muséum National d'Histoire Naturelle, Paris, from the Lower Cretaceous (Aptian) at Grandpré (Ardennes), France,  $\times 10$ . 63, *Pygaulus morloti* Desor: Phyllode of ambulacrum V of De Lorio's (1873, pl. 17, figs. 1, 3) figured specimen in the De Lorio Collection at the Muséum d'Histoire Naturelle, Genève, Switzerland, from the Lower Cretaceous (Neocomian) at La Russille, near Orbe, Switzerland,  $\times 10$ .

slightly larger than pores in plates beyond petals, details of pores not clear on specimens studied, but according to d'Orbigny's figures pores conjugate, slightly elongated transversely.

*Periproct*.—Marginal, longitudinal, with slight groove extending from periproct to adoral surface.

*Peristome*.—Anterior, higher than wide, pentagonal.

*Floscelle*.—Bourrelets well developed, inflated; phyllodes broad, double pored, two series of pore pairs in each half-ambulacrum, 9 or 10 in each outer series, 4 or 5 in each inner (text fig. 59); inner pore of each pore pair greatly reduced in size; no buccal pores.

*Occurrence*.—Cretaceous (Cenomanian), Bedoule, near Cassis, France.

*Location of type specimen*.—According to Cotteau (1860, p. 457) the holotype is in the collection of M. Barges.

*Remarks*.—Because of the great similarity of *C. bargesii* to the type species of *Catopygus*, *C. carinatus*, *Penesticta* is herein considered a junior subjective synonym of *Catopygus*. Both species are strikingly similar in shape and size, and have almost identical phyllodes with approximately the same number of pore pairs in each series, and in both species the inner pore is much smaller than the outer. They differ in that the petaloid pores are similar to each other in *C. bargesii*, whereas in *C. carinatus* the outer is elongated. Also, there are only three genital pores in *C. bargesii*, but four in *C. carinatus*.

Most authors including Mortensen (1948, p. 160) and Lambert and Thiéry (1921, p. 354) have considered *Penesticta* as a synonym of *Oolopygus*. They were not aware that *C. bargesii* has double-pored phyllodes, whereas the type species of *Oolopygus*, *O. gracilis*, has single pores in its phyllodes.

According to d'Orbigny's figures and Cotteau's description, there is a small pore in genital plate 2. On all the specimens I have seen, there is no pore in this genital plate.

#### Genus PHYLLOBRISUS Cotteau

*Phyllobrissus* Cotteau, 1859. Éch. foss., L'Yonne, vol. 2, p. 81. Type species, *Catopygus gresslyi* L. Agassiz, 1839, by subsequent designation, Cotteau, 1860 (Pal. franc., Crét.), p. 553.

Synonyms: *Anthobrissus* Pomel; *Asterobrissus* De Loriol.

#### GENERIC DESCRIPTION

Small, inflated, slightly angular marginal outline, with slightly truncated posterior margin, adoral surface flat or somewhat depressed,

greatest width and height often posterior to center; apical system anterior, tetrabasal, four genital pores; petals of approximately equal length, flush, open, or with slight tendency to close, with outer pore of pore pair more elongate than inner, all ambulacral plates double pored; periproct supramarginal or almost marginal, always at least slightly visible from above; often with groove extending from lower edge of periproct opening to adoral edge of test; peristome anterior, pentagonal, slightly higher than wide; bourrelets fairly well developed; phyllodes slightly broadened, with two series of double pores in each half-ambulacrum, approximately eight in each outer series, five in each inner; pore of each pair often reduced in size; no buccal pores.

*Comparison with other genera.*—*Phyllobrissus* is very similar to *Catopygus*, and it is difficult to decide whether or not this genus should be maintained. Lambert (1902, p. 15) and Mortensen (1948, p. 167) suggested that *Phyllobrissus* might be considered as a subgenus of *Catopygus*. Their type species are very similar in general appearance. Both have the same petal arrangement, strikingly similar phyllodes, with two series of pore pairs in each half-ambulacrum, and with the inner pore of each pair greatly reduced in size. They differ in that *P. gresslyi* is slightly broader, with a more depressed adapical surface, and an obliquely truncated posterior margin exposing the periproct adapically. In *C. carinatus* the posterior margin is pointed, and the periproct is not visible from above. Although these differences may be sufficient to distinguish generically these two species, there are some species which have some of the characters of both these species, and it is difficult to decide to which of the two genera to assign them.

*Phyllobrissus* is also very similar to *Nucleolites*, with both genera having narrow, straight, open petals, and very similar phyllodes. *Phyllobrissus* differs in having a more elongate test, more developed bourrelets, and a more marginal periproct.

*Remarks.*—Cooke (1953, p. 17, and 1955, p. 97) refers to *Phyllobrissus* two American species, *Petalobrissus cubensis* (Weisbord) and *Nucleopygus angustatus* (Clark). I do not agree with this assignment. *Petalobrissus cubensis* has a much more developed floscelle with single-pored phyllodes (text fig. 106) and buccal pores, as opposed to the double-pored phyllodes and lack of buccal pores in *Phyllobrissus*. Furthermore, the apical system in *Petalobrissus cubensis* is monobasal, whereas it is tetrabasal in *Phyllobrissus*.



*N. angustatus* has single-pored phyllodes and buccal pores, and therefore should not be referred to *Phyllobrissus*.

*Range and distribution*.—Upper Jurassic to Upper Cretaceous (Kimmeridgian to Senonian) of Europe, India, and United States.

#### DESCRIPTION OF TYPE SPECIES

##### PHYLLOBRISUS GRESSLYI (L. Agassiz)

Plate 11, figures 4, 5; text figures 60, 61

*Catopygus gresslyi* L. Agassiz, 1839, *Ech. foss. Suisse*, pt. 1, p. 49, pl. 8, figs. 1-3.

*Material*.—Three specimens studied in the Lambert Collection, Sorbonne, one in the d'Orbigny Collection in the Muséum National d'Histoire Naturelle, Paris, and one in the collections at the U. S. National Museum.

*Shape*.—Small, elongate, slightly angular marginal outline, greatest width and height posterior to center, posterior margin slightly truncated obliquely with surface visible adapically, adoral surface flat to slightly depressed.

*Apical system*.—Anterior, four genital pores, tetrabasal (text fig. 60), posterior genital plates in contact.

*Ambulacra*.—Petals narrow, equal length, open, with only slight tendency to close; petals II, III, and IV extending almost to margin, petals V and I over one-half distance to margin; interporiferous zones twice width of poriferous zones; pores slightly conjugate, outer pore elongated obliquely to round inner pore.

*Periproct*.—Supramarginal, but near margin, longitudinal, with groove extending from opening to ventral edge of test.

*Peristome*.—Anterior, pentagonal slightly higher than wide, slightly depressed.

*Floscelle*.—Bourrelets slightly developed; phyllodes double pored (text fig. 61), with two series of pore pairs in each half-ambulacrum: seven to nine pore pairs in each outer series, four to six in inner series; inner or lower pore of each pore pair much smaller than other pore.

*Occurrence*.—Neocomian of France and Switzerland.

*Location of type specimen*.—Unknown.

#### Synonym of PHYLLOBRISUS

*Anthobrissus* Pomel, 1883. *Class. méth.*, p. 60. Type species by subsequent designation, Mortensen (1948, p. 167), *Nucleolites cerceleti* Desor in Agassiz and Desor (1847, p. 155).



*Remarks.*—I have studied three specimens of the type species in the Lambert Collection at the Sorbonne, Paris. One of these specimens was figured by Lambert. His description of this species (1892, p. 84-89) is so thorough and accurate that it is not necessary to redescribe it here. I include photographs (pl. 11, figs. 6, 7) and a drawing of a phyllode (text fig. 62) of his specimen.

Duncan (1891, p. 187), Lamber and Thiéry (1921, p. 350), Mortensen (1948, p. 165, 167), and Cooke (1953, p. 17) have considered *Anthobrissus* a synonym of *Phyllobrissus*. Although it differs from the type species of *Phyllobrissus* in being more elongate, having slightly narrower petals, and in having its periproct more anterior, these differences do not seem of sufficient importance to warrant generic distinction.

#### Synonym of PHYLLOBRISSUS

*Asterobrissus* De Loriol, 1888. Mém. Soc. Phys. Hist. Nat. Genève, vol. 30, p. 104; pro *Trochalia* Pomel, 1883. Class. méth., p. 60; non Sharpe, 1850, a mollusk. Type species, *Echinobrissus requieni* Desor (in Agassiz and Desor, 1847) by subsequent designation, Kier, herein.

*Remarks.*—Because of the invalid designation of a type species, Lambert, Mortensen, and others have misunderstood this genus. Lambert (in Demoly and Lambert, 1913, p. 204) designated *Asterobrissus fourtani* as the type species of *Asterobrissus*. However, since this species was not included among those referred to *Trochalia* in Pomel's original description of the genus, or in De Loriol's description of *Asterobrissus*, it cannot be considered as the type species. Lambert stated that when Pomel erected his genus, and included *Echinobrissus requieni* Desor among its species, he was not referring to the typical *E. requieni* but to some specimens of another species which had been wrongly referred to *E. requieni*. Lambert named this other species *Asterobrissus fourtani* and designated it as the type species. Even though Pomel may have been referring to these specimens when he made his genus, he used the name *E. requieni* Desor, and it and the other species he and De Loriol named are the only ones that can be considered in selecting the type species.

I have not seen any specimens of *E. requieni*, but from a study of the illustrations by d'Orbigny (1856, pl. 963, figs. 6-10), it resembles closely the type species of *Phyllobrissus*, *P. gresslyi* (Agassiz), making *Asterobrissus* a synonym of *Phyllobrissus*. Most of the other species that Pomel referred to *Trochalia* should be placed in *Petalobrissus*. I have studied specimens of Lambert's *Asterobrissus fourtani*, and believe that this species is a *Phyllobrissus*. It is similar to *P. gresslyi* in petal arrangement, tetrabasal apical system, supra-

marginal periproct, and in having double-pored phyllodes and no buccal pores. It differs mainly in shape, being almost square in marginal outline, but this difference is not of sufficient importance to justify generic distinction of this species.

#### Genus PYGAULUS Agassiz

*Pygaulus* L. Agassiz in L. Agassiz and Desor, 1847. Am. Sci. Nat., ser. 3, vol. 7, p. 158. Type species by subsequent designation, Cotteau, 1869, Pal. franc., Jur., p. 124, *Pygaulus desmoulinii* Agassiz.

#### GENERIC DESCRIPTION

Medium size, elongate, sides usually parallel, anterior and posterior margins rounded, adapically highly inflated, cylinder shaped, apical system anterior, tetrabasal; petals broad, open or slightly closed, petal III shorter than others, poriferous zones narrow, tapering distally, pores conjugate, interporiferous zones very wide, all ambulacral plates double pored; periproct inframarginal, longitudinal; peristome large, oval or oblique; bourrelets slightly developed; phyllodes slightly widened or not widened, double pored, pores arranged in two series in each half-ambulacrum; no buccal pores; tubercles only slightly larger adorally.

*Comparison with other genera.*—*Pygaulus* is very similar to *Pygorhynchus*. Species of both genera have similar petals, an oblique peristome, phyllodes with approximately the same number of pore pairs in each series, and a longitudinal periproct. They are distinguished by the shape of the test and location of the periproct. In *Pygaulus*, the test is generally high, with a smoothly rounded anterior and posterior margin, parallel sides, and inframarginal periproct. In *Pygorhynchus*, the test is generally lower, the anterior margin is blunted, the posterior pointed, with the sides not parallel but expanding posteriorly, resulting in the greatest width being posterior to the center. The periproct is more marginal in position. These differences are not very significant, and there is little doubt that these two genera are closely related.

*Pygaulus* is also very similar to *Plagiochasma*, having an almost identical petal arrangement, peristome, and floscelle, but differing in having an inframarginal instead of supramarginal periproct, and a more cylindrical test.

*Remarks.*—I have included (text fig. 63) a drawing of a phyllode of *Pygaulus morloti* Desor. The specimen illustrated was figured by De Loriol (1873, pl. 17, figs. 1, 3) and is in his collection at the

Muséum d'Histoire Naturelle, Genève. De Loriol referred this species to *Botriopygus*=*Pygorhynchus*, but Lambert and Thiéry (1921, p. 339) placed it in *Pygaulus*. In its lower test, this species resembles *Pygorhynchus*, but its sides are parallel, both posterior and anterior margins are rounded, and its periproct is inframarginal—all characters of *Pygaulus*.

Included also are photographs (pl. 11, figs. 8, 9) of the holotype of *Pygaulus couzensis* Demoly and Lambert (1913, p. 201). This specimen is in the Lambert Collection at the Sorbonne, Paris.

*Range and distribution*.—Cretaceous (Neocomian to Cenomanian) of Europe.

#### DESCRIPTION OF TYPE SPECIES

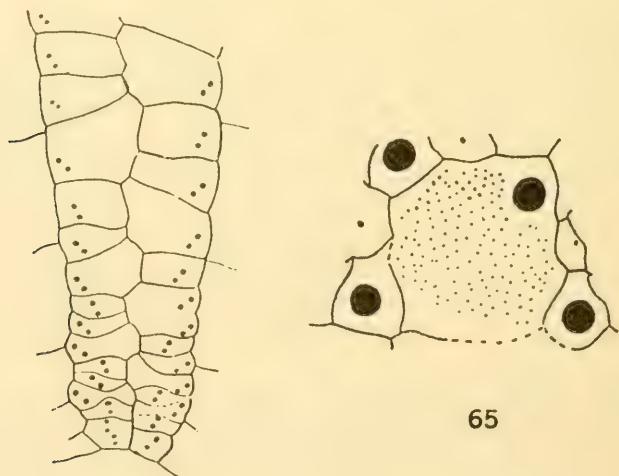
##### **PYGULUS DESMOULINSII** Agassiz

Plate 11, figures 10-12; text figures 64, 65

*Pygaulus desmoulinsii* L. Agassiz in L. Agassiz and Desor, 1847. Ann. Sci. Nat., ser. 3, vol. 7, p. 158.

*Material*.—Eight specimens studied in the collections of the U. S. National Museum; two in the Lambert Collection, Sorbonne, Paris.

*Shape*.—Medium size, elongate, with almost straight sides, cylindrical shaped, adorally highly inflated, in some specimens slightly



64

65

FIGS. 64, 65.—*Pygaulus desmoulinsii* Agassiz: 64, Phyllode of specimen in Lambert Collection, Sorbonne, Paris, from the Neocomian,  $\times 10$ ; 65, apical system of USNM 131259, from the Barremian at Lussan,  $\times 15$ .

higher posteriorly; margins evenly rounded, adorally slightly flattened around peristome.

*Apical system*.—Anterior, tetrabasal (text fig. 65), genital 2 large, extending posteriorly, separating posterior genital plates; other genital plates small.

*Ambulacra*.—Petals broad, open, petal III shorter than others, all extending over two-thirds distance from apical system to margin; interporiferous zones very wide, over twice width of poriferous zones, expanding distally; poriferous zones narrow, tapering distally, pores conjugate, outer elongate transversely, inner round; pore pairs in plates beyond petals.

*Adoral interambulacra*.—Plates regularly alternating, double series continuing to peristome.

*Periproct*.—Inframarginal, flush, longitudinal, at end of slight posterior prolongation.

*Floscelle*.—Bourrelets slightly developed; phyllodes double pored, not widened, slightly depressed, two series of pore pairs in each half-ambulacrum: five to six pore pairs in each outer series, four or five in each inner; in some specimens, alternate pore pairs in outer series in plates not extending to midline (text fig. 64); most of inner pore pairs in occluded plates.

*Tuberculation*.—Tubercles on adoral surface approximately same size as on adapical.

*Occurrence*.—Lower Cretaceous (Barremian) of France and Switzerland.

*Location of type specimen*.—Not known.

#### Genus PYGORHYNCHUS L. Agassiz

*Pygorhynchus* L. Agassiz, 1839. Éch. foss. Suisse, pt. 1, pp. 53, 99. Type species by subsequent designation, Lambert (1898, p. 162), *Catopygus obovatus* L. Agassiz.

Synonym: *Botriopygus* d'Orbigny.

#### GENERIC DESCRIPTION

Medium to large, usually with greatest width posterior to center, anterior margin blunt, posterior pointed, low, or in a few species moderately inflated; apical system tetrabasal, anterior, four genital pores; petals well developed, broad, slight tendency to close distally, narrow poriferous zones with conjugate pores, all ambulacral plates double pored; periproct marginal to inframarginal, longitudinal; peristome anterior, depressed, oblique or regular; bourrelets well





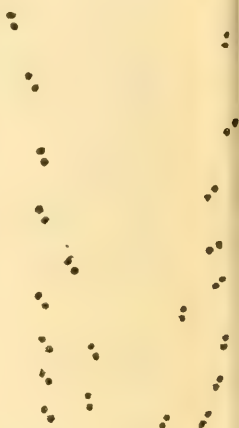
66



67



68



69



70



71



72

(See legend on opposite page.)



developed, phyllodes double pored, slightly broadened, with two series of pore pairs in each half-ambulacrum; 8 to 10 in each outer series, 3 to 5 in each inner; no buccal pores.

*Comparison with other genera.*—*Pygorhynchus* is very similar to *Pygaulus*, and probably closely related. Both genera have similar petals, an oblique peristome, phyllodes with approximately the same number of pore pairs in each series, and a longitudinal periproct. They differ in that the test in *Pygorhynchus* is generally lower, the anterior margin blunted, posterior pointed, and the sides not parallel as in *Pygaulus*, but diverging posteriorly. The periproct in *Pygorhynchus* is usually more marginal.

*Pygorhynchus* is also quite similar to *Parapygus*, from which it is distinguished by its double-pored phyllodes and its lack of buccal pores; as opposed to the single-pored phyllodes with buccal pores of *Parapygus*. As both these features in *Pygorhynchus* are more primitive, and as this genus occurs earlier in the Cretaceous, it is probable that *Pygorhynchus* is an ancestor of *Parapygus*.

*Remarks.*—Cotteau (1890, pp. 55, 56) says that the apical system is monobasal in *Pygorhynchus*. This error is probably due to the large central madreporite which gives the apical system the appearance of being monobasal.

As the phyllode structure has not been illustrated in most of the species of *Pygorhynchus*, I include a drawing of a phyllode of each of the following species: *P. minor* (Agassiz) (text fig. 66), *P. cylindricus* (Desor) (text fig. 67), *P. valdensis* (De Loriol) (text fig. 68—drawing of the lectotype, herein designated, figured by

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FIGS. 66-72.—66, *Pygorhynchus minor* (Agassiz): Phyllode of ambulacrum I of specimen in École National Supérieure des Mines, Paris, from Ste. Croix, France,  $\times 10$ . 67, *Pygorhynchus cylindricus* (Desor): Phyllode of ambulacrum I of specimen in École National Supérieure des Mines, Paris, from the Lower Cretaceous (Aptian) at Le Bimet, France,  $\times 10$ . 68, *Pygorhynchus valdensis* (De Loriol): Phyllode of ambulacrum II of De Loriol's (1873, pl. 16, fig. 2) figured specimen and lectotype in the De Loriol Collection, at the Muséum d'Histoire Naturelle, Genève, Switzerland, from the Lower Cretaceous (Valanginian) at Ballaigue (Vaud), Switzerland,  $\times 10$ . 69, *Pygorhynchus subinferus* (Desor): Phyllode of ambulacrum IV of De Loriol's (1873, pl. 18, fig. 9) figured specimen in the De Loriol Collection at the Muséum d'Histoire Naturelle, Genève, Switzerland, from the Lower Cretaceous (Valanginian), at Ballaigue (Vaud), Switzerland,  $\times 15$ . 70, *Pygorhynchus obovatus* (Agassiz): Phyllode of ambulacrum III of specimen in the Lambert Collection, Sorbonne, Paris, from the Lower Cretaceous (Neocomian) at Venoy, France,  $\times 15$ . 71, *Pygopistes coquandi* (Cotteau): Phyllode of ambulacrum III of the lectotype of *Pygopistes excentricus* (Gauthier), herein considered a synonym of *P. coquandi*, from the Cretaceous (Cenomanian) at El-Aieicha, Tunisia, in the Muséum National d'Histoire Naturelle, Paris,  $\times 15$ . 72, *Hypopygurus gaudryi* Gauthier: Phyllode of ambulacrum III of lectotype in Muséum National d'Histoire Naturelle, Paris, from the Cretaceous (Cenomanian) at Dj Cehela, Tunisia,  $\times 5$ .

De Loriol (1873, pl. 16, fig. 2) in the De Loriol Collection at the Muséum d'Histoire Naturelle, Genève, Switzerland), *P. subinferus* (Desor) (text fig. 69). It is interesting to note how similar to each other are the phyllodes of these different species.

Photographs of the adoral surface of *P. minor* and *P. cylindricus*, are on plate 12. Lambert's *Astrolampas romani* should be referred to *Pgorhynchus* as discussed on page 52.

Szörényi (1955a) has described many species which she refers to *Botriopygus*, from the Senonian of Bakony. Unfortunately, she does not include drawings of the phyllodes, but from the Senonian age of her species, it is probable that they have single-pored phyllodes and should be referred to *Parapygus*.

*Range and distribution.*—Cretaceous (Neocomian to Albian) of Europe, North Africa, and the Americas.

#### DESCRIPTION OF TYPE SPECIES

##### PYGORHYNCHUS OBOVATUS (L. Agassiz)

Plate 12, figures 1-5; text figure 70

*Catopygus obovatus* L. Agassiz, 1836a. Mém. Soc. Sci. Nat. Neuchâtel, vol. 1, p. 136.

*Material.*—The type specimens were believed lost according to Lambert and Jeannet (1928, p. 164), but I found them in the echinoid collections in the Museum of Comparative Zoology, Harvard. They are from the type locality, Mormont près La Sarraz, and were collected by L. Coulon. One of the specimens (herein designated the lectotype) is the specimen figured by Agassiz (1839, pl. 8, figs. 18-20). This figure is greatly restored, showing many details not visible on the specimen. Besides the type material, I have studied specimens in the Lambert Collection at the Sorbonne, Paris, at the d'Orbigny Collection at the Muséum National d'Histoire Naturelle, Paris, and material in the U. S. National Museum.

*Shape.*—Large (holotype 54 mm. long), low, greatest width posterior, anterior margin blunt, posterior pointed; depressed around peristome.

*Apical system.*—Anterior, madreporite large, extending posteriorly between posterior genital plates; four genital pores.

*Ambulacra.*—Well-developed petals extending almost to margin, with tendency to close distally, interporiferous zones wide, at maximum nearly twice width of poriferous zones, poriferous zones narrow, pores conjugate, outer pores of pore pairs slitlike, inner slightly elongated longitudinally.

*Periproct*.—Inframarginal, higher than wide, in slight adoral groove.

*Peristome*.—Oblique or regular, anterior.

*Floscelle*.—Bourrelets well developed; phyllodes (text fig. 70) with double pores, inner pore much smaller than outer on well-preserved specimens; pore pairs arranged in an outer and inner series in each half-ambulacrum with approximately 10 pore pairs in outer, 6 in inner; no buccal pores.

*Occurrence*.—Neocomian of France and Switzerland.

*Location of type specimen*.—Museum of Comparative Zoology, Harvard, No. 772.

*Remarks*.—There has been considerable controversy over whether or not the peristome is oblique or regular in this species. L. Agassiz (1839, pl. 8, fig. 19) figured it as regular, but d'Orbigny (1855, pl. 929, fig. 6) figured it as oblique. Agassiz had two specimens in his type lot, one with a regular peristome (the lectotype), and the other with an oblique peristome. It is possible that the shape of the peristome is variable within the species. Until a study has been made of a large population of this species, it is advisable to include in *Pygorhynchus* specimens with either an oblique or regular peristome.

#### Synonym of PYGORHYNCHUS

*Botriopygus* d'Orbigny, 1856. Pal. franc., Crétacé, vol. 6, p. 334. Type species by subsequent designation, Cotteau, 1869, Pal. franc., Jur., p. 121, *Catopygus obovatus* L. Agassiz.

*Remarks*.—*Botriopygus* is a junior, objective synonym of *Pygorhynchus*, having the same type species. Lambert and Thiéry (1921, p. 353) and Mortensen (1948, p. 143) are mistaken in considering *Botriopygus cotteauanus* d'Orbigny as the type species of *Botriopygus*. d'Orbigny did not designate a type species for his genus. Lambert's (1898, p. 162) designation of *B. cotteauanus* as the type species of *Botriopygus* is invalid because Cotteau (1869, Pal. franc., Jur., p. 121) had already designated *B. obovatus*. *B. cotteauanus* is the type species of *Parapygus* Pomel, 1883.

#### Genus PYGOPISTES Pomel

*Pygopistes* Pomel, 1883. Class. méth., p. 56. Type species by monotypy, *Catopygus floridus* Coquand (a nomen nudum)=*Pygaulus coquandi* Cotteau.

#### GENERIC DESCRIPTION

Small, highly inflated, with rounded margin, gently rounded sides, pulvinate adoral surface with peristome and phyllodes depressed;



apical system very eccentric anteriorly, tetrabasal, four genital pores; petals long, extending almost to margin, open, narrow poriferous zones, tapering distally, pores conjugate, outer elongate transversely; all ambulacral plates double pored; periproct marginal, elongate longitudinally; peristome anterior, oblique, large, depressed; bourrelets slightly developed; phyllodes slightly broadened, double pored, two series of pore pairs in each half-ambulacrum; no buccal pores, no naked sternal area.

*Comparison with other genera.*—Lambert and Thiéry (1921, p. 340) and Mortensen (1948, pp. 141, 143) consider *Pygopistes* as a synonym of *Pygorhynchus*. However, the two genera are quite distinct. In *Pygopistes* the test is much more inflated, with steeper sides, a more rounded marginal outline and a more pulvinate adoral surface. The apical system is much more eccentric anteriorly in *Pygopistes*, and there are fewer pore pairs in the phyllodes.

The type species of *Pygopistes* and *Plagiochasma* are very similar, both having an oblique peristome, similar phyllodes and petals, but they differ in that in *Pygopistes coquandi* the test is more inflated, and the periproct is marginal. *Pygopistes* differs from *Pygaulus* in having a more anteriorly eccentric apical system, and a more highly inflated test.

*Range and distribution.*—Cretaceous (Cenomanian) of North Africa.

#### DESCRIPTION OF TYPE SPECIES

#### PYGOPISTES COQUANDI (Cotteau)

Plate 13, figures 1-6; text figure 71

*Pygaulus coquandi* Cotteau, 1869, Rev. Mag. Zool., ser. 2, vol. 21, pp. 243-245, pl. 13, figs. 1-4.

*Material.*—Specimens were studied in the De Loriol Collection at the Muséum d'Histoire Naturelle at Genève, in the Cotteau Collection at the École des Mines, Paris, and in the Muséum National d'Histoire Naturelle, Paris.

*Shape.*—Small, 25 mm. long, elongate, marginal outline smoothly rounded, right anterior margin slightly prolonged, extending farther anteriorly than left anterior margin, right posterior margin slightly more prolonged than left; test highly inflated, in some specimens greatest height anterior to center, in others near center; adoral surface slightly pulvinate with phyllodes and peristome slightly depressed.

*Apical system*.—Very eccentric anteriorly, four genital pores, tetrabasal, posterior genital plates separated by genital 2.

*Ambulacra*.—Petals open, long, extending almost to margin, posterior petals longer than others; poriferous zones narrow, tapering distally, one-half width of interporiferous zones; pores strongly conjugate, outer pore of pair elongated transversely, inner round.

*Periproct*.—Marginal, slightly visible from above, elongated longitudinally.

*Peristome*.—Large, anterior, depressed, oblique with long axis extending from posterior right to anterior left.

*Floscelle*.—Bourrelets slightly developed; phyllodes (text fig. 71) slightly broadened, depressed, double pored with two series of pore pairs in each half-ambulacrum: eight pore pairs in each outer series, four or five in each inner; no buccal pores.

*Occurrence*.—Cretaceous (Cenomanian) of Algeria and Tunisia.

*Location of type specimen*.—According to Cotteau, the type specimen is in the Coquand Collection.

*Remarks*.—The figures of *Pygopistes coquandi* in Cotteau, Peron, and Gauthier (1879, pl. 10, figs. 7-12) are not accurate. They show a test with a symmetrical marginal outline, whereas the right anterior margin projects more anteriorly than the left. Furthermore, the apical system is depicted as being almost central, whereas it is very eccentric anteriorly, and the periproct is shown to be lower than it really is. Perhaps because of these inaccuracies, Gauthier (1889a, p. 36) erected a new species, *Pygopistes excentricus* for specimens that are herein believed to be conspecific with *P. coquandi*. Gauthier's lectotype (herein designated) is in the Muséum National d'Histoire Naturelle, Paris. I include photographs of it (pl. 13, figs. 4-6). In Gauthier's figure he shows the periproct far more anterior than it really is.

#### Genus HYPOPYGURUS Gauthier

*Hypopygurus* Gauthier, 1889a. Ech. foss., Tunisie, pp. 37, 38. Type species by monotypy, *Hypopygurus gaudryi* Gauthier.

#### GENERIC DESCRIPTION

Medium to large, low, elongate with pointed posterior margin, adoral surface concave; apical system anterior, tetrabasal with four genital pores; petals broad, open, with straight poriferous zones, petals I and V longer than others, pores conjugate, outer pore slitlike, all ambulacral plates double pored; periproct inframarginal, elongate



longitudinally; peristome anterior, pentagonal; bourrelets well developed, inflated; phyllodes broadened, double pored, with pore pairs in two series in each half-ambulacrum: 10 to 12 pore pairs in each outer series, 4 to 6 in each inner; single buccal pores.

*Comparison with other genera.*—*Hypopygurus* is most similar to *Pygorhynchus*, having large petals, an inframarginal periproct, and similar phyllodes. It differs in having buccal pores and straighter poriferous zones. Lambert and Thiéry (1921, p. 357) considered *Hypopygurus* as a subgenus of *Astrolampas*, but the petals in *Hypopygurus* have straight poriferous zones, not lanceolate as in *Astrolampas*, the apical system is more eccentric anteriorly, and it has buccal pores.

*Range and distribution.*—Cretaceous (Cenomanian) of Tunisia; only one species known.

#### DESCRIPTION OF TYPE SPECIES

#### HYPOPYGURUS GAUDRYI Gauthier

Plate 13, figures 7, 8; text figure 72

*Hypopygurus gaudryi* Gauthier, 1889a. Ech. foss., Tunisie, pp. 38-39, pl. 2, figs. 19-23.

*Material.*—Three specimens were studied in the Lambert Collection at the Sorbonne, and two in the Muséum National d'Histoire Naturelle, Paris. The specimen figured by Gauthier in his plate 2, figures 22, 23, is herein designated as the lectotype.

*Shape.*—Medium to large (largest specimen 61 mm. long), low, elongate with pointed posterior margin; adoral surface depressed.

*Apical system.*—Anterior, tetrabasal with large genital plates.

*Ambulacra.*—Petals broad, long, extending almost to margin, petals I and V longer than others, straight, or slightly curved in some specimens, widely open; interporiferous zones wide, increasing in width distally; poriferous zones wide, tapering distally; pores strongly conjugate, outer pore slitlike, inner round to slightly elongate transversely.

*Periproct.*—Inframarginal, oval, elongated longitudinally.

*Peristome.*—Anterior, pentagonal, slightly higher than wide.

*Floscelle.*—Bourrelets well developed, inflated; phyllodes broadened, double pored (text fig. 72) with pore pairs arranged in two series in each half-ambulacrum: 10 to 12 in each outer series, 4 to 6 in each inner; single buccal pores present.

*Occurrence.*—Cretaceous (Cenomanian), Djebel Cehela, Tunisia.

*Location of type specimen.*—Lectotype in the Muséum National d'Histoire Naturelle, Paris.

*Remarks.*—Gauthier's figure of the adapical surface is inaccurate, as it shows very flexuous petals with highly curved poriferous zones. In most of the specimens the petals are straight, in a few they are only slightly curved.

Mortensen (1948, p. 189) states that "the apical system is not tetrabasal, but evidently not clearly monobasal either." Evidently he based this conclusion on Gauthier's figures of the apical system in which the suture lines are not clear. However, in his description, Gauthier states that although the sutures are not visible on all the specimens, they are visible on the well-preserved specimens. On one of the specimens in the Lambert Collection, I found distinct sutures.

#### Genus *PLAGIOCHASMA* Pomel

*Plagiochasma* Pomel, 1883. Class. méth., p. 59. Type species by subsequent designation, Melville (1952, p. 1), *Nucleolites olfersii* L. Agassiz.

Synonyms: *Dochmostoma* Duncan; *Trematopygus* d'Orbigny.

#### GENERIC DESCRIPTION

Small to medium, elongate, anterior outline smoothly rounded, posterior usually slightly indented by anal groove, greatest width usually posterior to center, adoral surface smoothly rounded marginally, depressed at peristome; apical system tetrabasal, four genital pores; petals usually unequal with petals V and I longer than others, interporiferous zones wide, poriferous zone narrow, equal length in each petal, with slight tendency to close distally, all ambulacral plates double pored; periproct supramarginal, longitudinal, in groove extending from opening to posterior margin; peristome usually oblique, anterior; bourrelets absent or slightly developed; phyllodes not widened or only slightly widened, double pored, pore pairs arranged in two series in each half-ambulacrum; no buccal pores; tubercles on adoral side only slightly larger than on adapical; no naked sternal area.

*Comparison with other genera.*—*Plagiochasma* is very similar to *Pygaulus* and probably closely related. In both genera the petals are open or only slightly closed, with wide interporiferous zones, narrow poriferous zones, often oblique peristome, slightly developed or absent bourrelets, and double-pored phyllodes with the pore pairs arranged in two series in each half-ambulacrum. *Plagiochasma* differs in having a supramarginal periproct, and a less anterior apical system.

*Plagiochasma* is also very similar to *Pygopistes*, both genera having similar petals, oblique peristome, and similar floscelle. However, in *Plagiochasma* the test is lower, and the periproct is supramarginal.

Lambert and Thiéry (1921, p. 339) include among the species they refer to *Trematopygus* (= *Plagiochasma*), Fourtau's (1913, p. 62) *Trematopygus aegyptiacus*. Fourtau (1921, p. 62) later transferred this species to *Botriopygus*. It is certainly not a *Plagiochasma* as shown by its marginal to inframarginal periproct, and monobasal apical system, but probably is a *Parapygus*. Fourtau in this same work described a *Plagiochasma*, *P. sinaeus* (Fourtau) from the Cenomanian of Egypt.

Lambert and Thiéry referred Clark's *Echinobrissus texanus* from the Coniacian Austin Chalk of Texas to *Trematopygus* (= *Plagiochasma*). Later, Cooke (1953, p. 13) placed this species in *Nucleopygus*. I have studied the holotype and agree with Lambert and Thiéry that the species is a *Plagiochasma*. Its shape, petal arrangement, position of periproct, and phyllodes are typical of that genus. Apparently its peristome is also oblique, but this area is not well preserved on the holotype. Its phyllodes are definitely double pored and very similar to those of *P. olfersii* whereas in *Nucleopygus* they are single pored.

I studied a specimen of *Plagiochasma excentricus* (Pictet and Renevier) in the De Loriol Collection at the Muséum d'Histoire Naturelle in Genève, Switzerland, and include a drawing (text fig. 73) of one of its phyllodes. It is of interest to note that the phyllode is slightly widened, whereas in *P. olfersii* the outer pore series is straight.

Melville (1952) described a new species of *Plagiochasma*, *P. coxwellense*, from the Aptian, Lower Greensand in England, including several excellent, detailed drawings of the plate structure. Zázvorka (1953) reported a new species, *Plagiochasma novaki* (Zázvorka), from the Lower Turonian of Bohemia.

*Range and distribution*.—Cretaceous (Neocomian to early Senonian) of Europe, Egypt, and the United States.

#### DESCRIPTION OF TYPE SPECIES

#### PLAGIOCHASMA OLFERSII (L. Agassiz)

Plate 14, figures 1-3; text figures 74-76

*Nucleolites olfersii* L. Agassiz, 1836a. Mem. Soc. Sci. Nat. Neuchâtel, vol. 1, p. 133, pl. 14, figs. 2, 3.

*Material*.—Sixteen specimens studied in the Museum of Comparative Zoology, Harvard, two in the d'Orbigny Collection at the Muséum



National d'Histoire Naturelle, one in the École National Supérieure des Mines, Paris, and one in the U. S. National Museum.

*Shape*.—Small to medium, up to 30 mm. long, elongate, smoothly curved anterior outline, slightly truncated posterior, sides expanding posteriorly with greatest width posterior to center; adapically inflated anteriorly, with steeply sloping anterior surface, gradually sloping posterior; adorally depressed around peristome, ambulacra slightly depressed, ambulacrum III more depressed than others.

*Apical system*.—Very eccentric anteriorly, tetrabasal (text fig. 74), genital plate 2 extending posteriorly, separating genital plates 1 and 4; ocular plates very large, ocular plates I and V in contact.

*Ambulacra*.—Petals broad, flush, unequal in length, petal III shortest, petals V and I longest, in specimen 22 mm. long: 32 pore pairs in poriferous zone of petal III, 36 in petals II or IV, 47 in V or I; petals slightly closing distally, petal III more open than others; interporiferous zones very wide, twice width of poriferous zones; poriferous zones taper distally, of equal length in same petal, pores conjugate, outer pores elongated transversely, inner round.

*Adoral interambulacra*.—Single plate (text fig. 75) at peristome, preceded by regularly alternating plates.

*Periproct*.—Supramarginal, longitudinal pointed anteriorly, expanding and smoothly rounded posterior; in groove extending to posterior margin.

*Peristome*.—Large, depressed, anterior, oblique, with long axis extending from left anterior to right posterior.

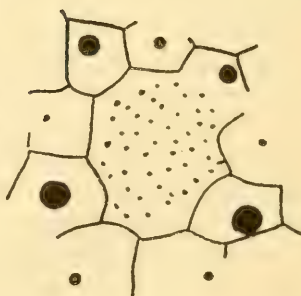
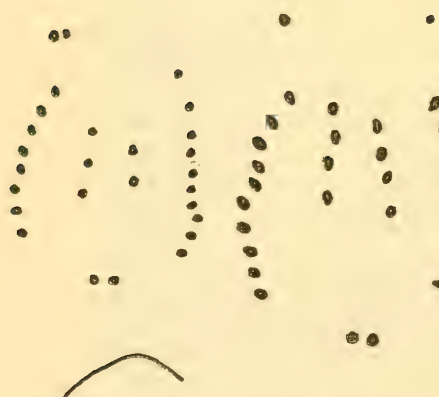
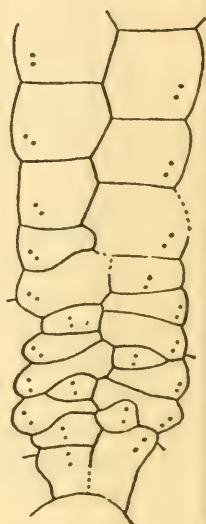
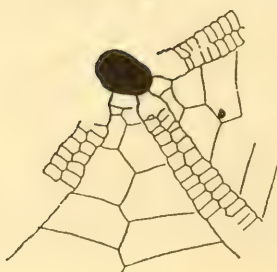
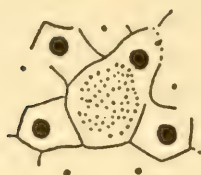
*Floscelle*.—Bourrelets slightly developed; phyllodes (text fig. 76) narrow to slightly widened, double pored with two series of pore pairs in each half-ambulacrum: five to seven pore pairs in each outer series, three to five in each inner; no buccal pores.

*Tuberculation*.—Adorally tubercles slightly larger than adapically.

*Occurrence*.—Lower Cretaceous (Hauterivian) of France and Switzerland.

*Location of type specimen*.—Not known.

*Remarks*.—d'Orbigny (1857, p. 374, pl. 949, fig. 7) described and figured a fifth imperforate supplementary plate in *Plagiochasma olfersii*. Wright (1875, Cretaceous, p. 252) mentioned this plate in his generic description, but presumably he was basing his description in part on d'Orbigny's, because he does not report this plate in his description of the apical system in *Plagiochasma faringdonense* Wright. This plate was not present on any specimens I studied of *P. olfersii*, and Melville (1952, p. 4) did not find it on any specimens



(See legend on opposite page.)



of *P. corwellense* Melville or of *P. faringdonense*. The posterior ocular plates are very large in *P. olfersii* (text fig. 74), and it is probable that d'Orbigny mistook one of them for a supplementary plate.

### Synonyms of *PLAGIOCHASMA*

*Dochmostoma* Duncan, 1891. Journ. Linn. Soc. (Zool.), vol. 23, p. 176. Type species herein designated, *Nucleolites olfersii* L. Agassiz.

*Remarks.*—*Dochmostoma* is a junior objective synonym of *Plagiochasma*, both genera having the same type species. Duncan created this genus because he did not like the name *Trematopygus*.

*Trematopygus* d'Orbigny, 1857. Pal. franc., Crétacé, vol. 6, p. 374; non Holmgren (1855, K. Svensk. Vetensk. Akad. Handl., N. F., vol. 1, p. 179; a genus of Hymenoptera). Type species: *Nucleolites olfersii* Agassiz by subsequent designation, Lambert and Thiéry (1921, p. 338).

### Genus *OOLOPYGUS* d'Orbigny

*Oolopygus* d'Orbigny, 1856. Pal. franc., Crétacé, vol. 6, atlas, pls. 976-977.

Type species, *Oolopygus gracilis* Lambert=*Oolopygus pyriformis* d'Orbigny 1856, non *Oolopygus pyriformis* (Leske, 1778), by subsequent designation, Cotteau (in d'Orbigny 1860, p. 458).

Synonym: ? *Pseudonucleus* Lambert.

### GENERIC DESCRIPTION

Small to medium size, elongate, with or without pointed posterior margin, inflated, with steep sides; apical system tetrabasal, anterior, three or four genital pores (no pore in genital 3 in some species), petals slightly developed, flush, equal, often difficult to discern, pores of pore pair equal, or outer elongated transversely, ambulacral plates beyond petals single pored; periproct marginal, longitudinal, often with

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FIGS. 73-80.—73, *Plagiochasma excentricus* (Pictet and Renevier): Phyllode of ambulacrum II from specimen in De Loriol Collection, at the Muséum d'Histoire Naturelle, Genève, Switzerland, from the Lower Cretaceous (Aptian) at Boveresce (Neuchâtel), Switzerland,  $\times 15$ . 74-76, *Plagiochasma olfersii* (Agassiz): 74, Apical system of specimen in Roman Collection from the Lower Cretaceous (Hauterivian), at Devecey (Doubs), France,  $\times 15$ ; 75, 76, adoral plate arrangement ( $\times 2$ ) and phyllode of ambulacrum V ( $\times 15$ ) of USNM 21814, from Lower Cretaceous (Neocomian) at St. Croix, Switzerland. 77, *Oolopygus gracilis* Lambert: Phyllode of ambulacrum V of Lambert's (1900, pl. 1, figs. 17-18) figured specimens in the Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Maestrichtian), Fresville, France,  $\times 15$ . 78, *Oolopygus pyriformis* (Leske): Phyllode of ambulacrum I of Lambert's figured specimen in the Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Maestrichtian) at Fresville (Manche), France,  $\times 15$ . 79, 80, *Pseudonucleus malladai* Lambert: 79, Apical system of holotype in Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Campanian) of Roiz, Santander, Spain,  $\times 21$ ; 80, phyllode of ambulacrum III of same specimen,  $\times 21$ .

slight groove extending from margin of periproctal opening to lower edge of test; peristome central to slightly anterior, higher than wide, pentagonal; floscelle well developed with strong bourrelets and broad, single-pored phyllodes with two series of pores in each half ambulacrum with 8 to 10 pores in the outer series, 2 to 4 in the inner; buccal pores present.

*Comparison with other genera.*—*Oolopygus* is very similar to *Catopygus* in general appearance, both having a small, elongate test with narrow, equal petals with pores of a pore pair either equal or the outer pore elongated transversely. The periproct is longitudinal and similarly located on the margin, and in both genera the peristome is higher than wide and pentagonal. They differ in that *Catopygus* has double pores in the phyllodes and no buccal pores, whereas *Oolopygus* has single-pored phyllodes and buccal pores. *Oolopygus* occurs later in the Cretaceous than most of the species of *Catopygus* and is clearly a descendant of *Catopygus* as shown by its more advanced phyllodes.

*Remarks.*—There has been considerable confusion over the nomenclature of the type species of this genus. There are two species from the Maestrichtian of Belgium which are very similar, and one of these is the type species. Leske (1778) described, but very poorly figured, *Echinites pyriformis*. Goldfuss (1826, p. 141) referred some specimens to Leske's *E. pyriformis*, but some authors have not considered his specimens conspecific with Leske's. d'Orbigny (1856, pls. 976-977) in the plates for "Paléontologie française, terrain Crétacé," figured and named two new species in his new genus *Oolopygus*, *O. bargesi* and *O. pyriformis*. d'Orbigny, in the same work, had placed *Echinites pyriformis* Leske in *Catopygus*. Cotteau (1860, p. 457), in the text for "Paléontologie française, terrain Crétacé," incorrectly credits Goldfuss with the authorship of *O. pyriformis* and designates it as the type species of *Oolopygus*. Later (1869, Pal. franc., Jur., p. 124) he stated that *Oolopygus bargesii* was the type species. Lambert (1909, p. 20) erected a new species, *Oolopygus gracilis*, for *O. pyriformis* d'Orbigny, non *Echinites pyriformis* Leske. *Echinites pyriformis* is also an *Oolopygus* and is a senior homonym of d'Orbigny's *O. pyriformis*.

Mortensen (1948, p. 160) considered *Oolopygus* as a subgenus of *Catopygus*. The presence of single pores in the phyllodes and the presence of buccal pores distinguishes this genus from *Catopygus*. Mortensen evidently was not aware of this difference in the phyllodes.

I have included photographs of Lambert's figured specimen of

*O. pyriformis* (pl. 29, figs. 7-9) and a drawing (text fig. 78) of one of its phyllodes.

*Range and distribution.*—Upper Cretaceous (Senonian) of France, Belgium, and Holland. *Oolopygus affinis* Sorignet occurs in the Pisolitic limestone which some authors consider to be Montian.

*Oolopygus williamsi* (Clark) from the Middle Maestrichtian of New Jersey may be a *Catopygus*. The holotype, and only known specimen, is an internal cast, and it is not possible to know whether or not it had single- or double-pored phyllodes.

#### DESCRIPTION OF TYPE SPECIES

##### *OOLOPYGUS GRACILIS* Lambert

Plate 29, figures 5, 6; text figure 77

*Oolopygus gracilis* Lambert, 1909. Bull. Soc. Linn. Normandie, ser. 6, vol. 2, pp. 20-21, pl. 1, figs. 17-18. *O. gracilis* is a substitute name for *Oolopygus pyriformis* d'Orbigny, 1856, Pal. franc., Crétacé, vol. 6, atlas, pl. 977, non *Oolopygus pyriformis* (Leske), 1778.

*Material.*—I have studied and photographed Lambert's figured specimen, which is in his collection in the Sorbonne, Paris.

*Shape.*—Small, Lambert's specimen 23 mm. long, d'Orbigny's 27 mm.; elongate, posterior margin slightly truncated in Lambert's specimen, but prolonged in d'Orbigny's; adapical surface smoothly inflated, adoral surface flattened; greatest width and height posterior to center.

*Apical system.*—Anterior, apparently tetrabasal although sutures not clear; tetrabasal system seen in specimen of *O. pyriformis* Leske, a species very similar to *O. gracilis*. Three genital pores, no pore in left anterior genital plate 3.

*Ambulacra.*—Petals slightly developed, equal in length, narrow, open, flush with test. Poriferous zones very narrow, one-half width of interporiferous zones; pores of pore pair equal, slightly elongated transversely.

*Periproct.*—Marginal, oval, longitudinal, with slight groove extending from opening to ventral edge of test.

*Peristome.*—Anterior, depressed slightly higher than wide, pentagonal.

*Floscelle.*—Bourrelets and phyllodes strongly developed. Phyllodes broad, single pored, with two series of pores in each half ambulacrum: 8 to 10 pores (text fig. 77) in each outer series, 2 to 4 in each inner. Two rows of sphaeridia in each ambulacrum; buccal pores present.

*Occurrence*.—Upper Cretaceous (Maestrichtian), Fresville, (Manche), France; Kunraad, Belgium.

*Location of type specimen*.—According to Cotteau (1860, Pal. franc., Crétacé, p. 458), the holotype is in the d'Orbigny Collection at the Muséum National d'Histoire Naturelle, Paris.

*Remarks*.—Further work is necessary on this species. d'Orbigny's figures of the holotype show a specimen differing in some characters from Lambert's specimens. Lambert's (1909, pl. 1, figs. 17, 18) specimen from Fresville (figured on my pl. 29, figs. 5, 6) has a slightly truncated posterior margin, whereas, according to d'Orbigny's figure, the posterior margin in the holotype is prolonged. The specimen that Lambert (1911c, pl. 2, figs. 22-25) figured from Kunraad is much more elongate than d'Orbigny's specimen, and has its greatest width anterior to the center instead of posterior as in d'Orbigny's specimen. Perhaps Lambert's specimens are not conspecific with d'Orbigny's. A reexamination of d'Orbigny's specimen should make possible a decision on this question. It is interesting to note that Lambert's figured specimen of *O. pyriformis* (Leske) (figured in my pl. 29, figs. 7-9) is much more similar in shape to d'Orbigny's holotype of *O. gracilis*. It differs in having the outer pore of a pore pair greatly elongated transversely, whereas it is almost round in *O. gracilis*. It is possible that *O. pyriformis* (Leske) and *O. gracilis* are conspecific, and the study of many specimens should clarify this situation.

d'Orbigny shows double pores in the ambulacral plates beyond the petals. This is an error on the part of the artist, as these pores are not paired.

#### ? Synonym of *OOLOPYGUS*

*Pseudonucleus* Lambert, 1920c. Ann. Soc. Linn. Lyon, vol. 66, p. 17. Type species by monotypy, *Pseudonucleus malladai* Lambert.

#### DESCRIPTION OF TYPE SPECIES

##### *PSEUDONUCLEUS MALLADAI* Lambert

Plate 44, figures 6-8; text figures 79, 80

*Pseudonucleus malladai* Lambert, op. cit., p. 17.

*Material*.—The holotype and one topotype were studied in the Lambert Collection at the Sorbonne, Paris. Both specimens are very small and poorly preserved, being fractured, weathered, and partially coated with secondary calcite.



*Shape*.—Small, holotype 11 mm. long, topotype 15 mm., elongate, with smooth marginal outline except for slight posterior truncation; adapical surface highly inflated, with steep sides, greatest height posterior to center; adoral surface flattened, peristome flush.

*Apical system*.—Anterior (text fig. 79), tetrabasal, four genital pores.

*Ambulacra*.—All ambulacra petaloid, petals narrow, very short, perhaps reflecting immaturity of specimens. Details of pores not visible.

*Periproct*.—Marginal, in center of posterior truncation.

*Peristome*.—Anterior, pentagonal.

*Floscelle*.—Bourrelets with vertical sides. Phyllodes definitely developed with slight crowding of single pores; buccal pores present (text fig. 80).

*Occurrence*.—Upper Cretaceous (Campanian) of Roiz (Santander), Spain.

*Remarks*.—Lambert believed that ambulacrum III was nonpetaloid in the type species of his *Pseudonucleus*. If this was so, then he was justified in erecting a new genus for it. However, I have studied under high magnification the holotype and one topotype in his collection and found that ambulacrum III is petaloid. In the holotype, the area where ambulacrum III occurs is badly eroded, and if it had been petaloid, there would have been no way to have known it. In a second topotypic specimen, ambulacrum III is definitely petaloid, and there is no question that this specimen is conspecific with the holotype. Lambert does not mention this second specimen in his description and it is possible that he received it after describing this species. In his original description Lambert states that the pores are not conjugate in the petals, but Lambert and Thiéry (1921, p. 358) say that they are conjugate. The specimens are so badly weathered and details of the test so obscured by secondary growth that I was unable to discern whether they were conjugate or not.

Lambert considered this species similar, except for its ambulacrum III, to *Oolopygus* or *Catopygus*. In its shape with its smoothly elongate, highly inflated test, it is very similar to *Oolopygus*. It is similar in having its apical system very eccentric anteriorly, in its inconspicuous petals and location of its periproct. Unfortunately, the two and only known specimens of *Pseudonucleus* are very small and may show immature characters. It therefore seems advisable to consider *Pseudonucleus* only tentatively as a synonym of *Oolopygus*.



Genus **HEMICARA** Schlüter

*Hemicara* Schlüter, 1902. Zeitschr. Deutsch. Geol. Ges., vol. 54, p. 332. Type species by monotypy, *Hemicara pomeranum* Schlüter.

## GENERIC DESCRIPTION

Medium size, highly inflated, flat adoral surface; apical system tetrabasal, four genital pores; petals very slightly developed, narrow; all ambulacral plates double pored; periproct inframarginal, transverse; peristome pentagonal, width equal to height; bourrelets strongly developed, inflated; phyllodes widened, double pored; no buccal pores; narrow naked median zone in interambulacrum 5 adorally.

*Comparison with other genera.*—*Hemicara* is easily distinguished from all the other genera of the Nucleolitidae and may not belong to this family. It resembles some species of *Catopygus* by its floscelle and slightly developed petals but can be distinguished easily by its broader test and inframarginal periproct.

*Range and distribution.*—Upper Cretaceous (Senonian) of Poland and Germany; only one species known.

## DESCRIPTION OF TYPE SPECIES

**HEMICARA POMERANUM** Schlüter

Plate 22, figures 1-3

*Hemicara pomeranum* Schlüter, 1902. Zeitschr. Deutsch. Geol. Ges., vol. 54, p. 332, pl. 11, figs. 5-10.

*Material.*—Professor Kongiel sent me photographs of a well-preserved specimen in his collection.

*Shape.*—Medium size, elongate, broad, with rounded anterior margin, slightly pointed posterior, highly inflated with steep side, adoral surface flat, peristome flush.

*Apical system.*—Anterior, tetrabasal, four genital pores.

*Ambulacra.*—Petals slightly developed, narrow, open, extending almost to margin.

*Periproct.*—Inframarginal, transverse.

*Peristome.*—Anterior, pentagonal, width equal to height.

*Floscelle.*—Bourrelets well developed, swollen; phyllodes widened, double pored, with two series of pore pairs in each half-ambulacrum; no buccal pores.

*Tuberculation.*—Naked zone in medial zone in interambulacrum 5 adorally.

*Occurrence*.—Upper Cretaceous (Senonian) of Germany and Poland.

*Location of type specimen*.—Not known by this author.

### Family ECHINOLAMPADIDAE Gray, 1851

Medium to large, elongate to circular, usually highly inflated; apical system tetrabasal or monobasal; periproct marginal to inframarginal, transverse or longitudinal; peristome transverse; petals long, usually broad, open, usually with poriferous zones of unequal length in the same petal, in earlier genera outer pore slitlike, single pores in ambulacral plates beyond petals; bourrelets well developed; phyllodes widened, single pored, with few or many pores; buccal pores present; tubercles adorally only slightly larger; narrow, naked, granular zone in interambulacrum 5.

*Genera*.—*Parapygus*, *Arnaudaster*, *Echinolampas*, *Plesiolampas*, *Conolampas*.

*Range*.—Cretaceous (Cenomanian) to Recent.

*Comparison with other families*.—The Echinolampadidae differ from the Faujasidae in having less developed bourrelets and more open petals, with poriferous zones in the same petal of unequal length. They differ from the Pliolampadidae in having narrower poriferous zones of unequal length, and in having a naked granular zone in interambulacrum 5.

### Genus PARAPYGUS Pomel

*Parapygus* Pomel, 1883. Class. méth., p. 61. Type species by subsequent designation, Lambert, 1898, p. 162, *Botriopygus cotteauanus* d'Orbigny.

Synonyms: *Pseudocatopygus* Cotteau and Gauthier; *Rostropygus* Szörényi.

### GENERIC DESCRIPTION

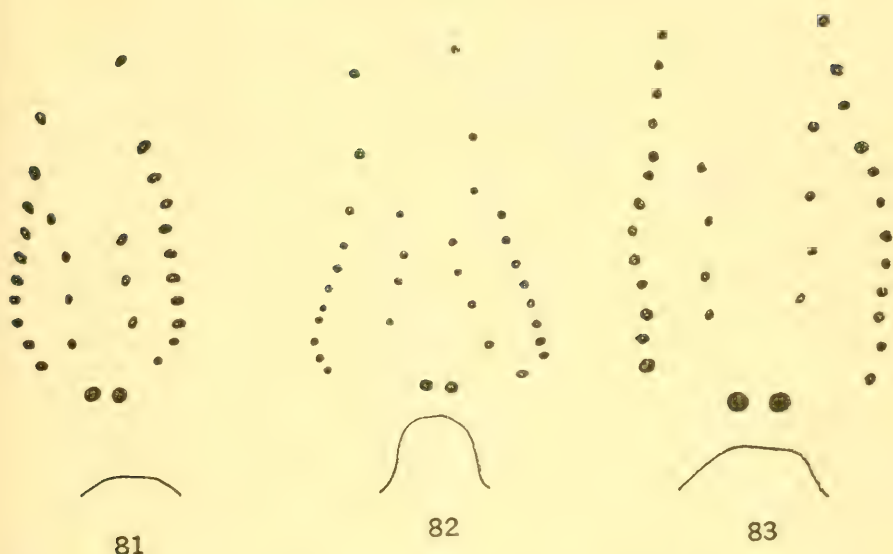
Medium to large, elongate somewhat inflated, with well-rounded margin, slightly depressed adoral surface; apical system tetrabasal anterior, with four genital pores, posterior genital plates separated by genital 2; petals well developed, open or with slight tendency to close distally, pores conjugate; single pores in ambulacral plates beyond petals; periproct marginal, longitudinal; peristome anterior, regular, pentagonal, wider than high; bourrelets well developed, extending convexly into peristome; phyllodes single pored, broadened, two or rarely three rows of pores in each half-ambulacrum, approximately 10 in each outer series, 3 or 4 in each inner, 1 to 3 in each median series; buccal pores present.

*Comparison with other genera.*—This genus is very similar to *Pygorhynchus* in most characters except that the phyllodes are single pored in *Parapygus* but double pored in *Pygorhynchus*. *Parapygus* is probably a descendant of *Pygorhynchus*. It occurs later in the Cretaceous, and its single-pored phyllodes indicate that it is more advanced.

*Remarks.*—According to Mortensen (1948, p. 144) the apical system may be tetrabasal or monobasal, because Checchia-Rispoli (1914, p. 7; 1931, p. 17) reports a monobasal apical system in two species he refers to *Botriopygus*, *B. tripolitanus* (Krumbeck) and *B. milloscewichi* Checchia-Rispoli. However, even if it is correct that the apical systems are monobasal in these species, it is not certain that they belong in the genus *Parapygus*. The shape of their tests and the arrangement of their petals is not typical of *Parapygus*. In all the species of *Parapygus* in which I have been able to see the apical system, it has been tetrabasal, and until these supposedly monobasal species have been reexamined, it seems best to consider *Parapygus* as a tetrabasal genus.

As most of the species of this genus have never been well figured, I include pictures and drawings of several of the species. In the École des Mines, I found what is probably Cotteau's figured specimen of *P. nanclasi* (Coquand). A picture of its adapical surface and a picture of the adoral surface of another specimen from the same locality is on plate 15, figures 8, 9. A drawing of a phyllode is on text figure 81. Cotteau in his figure 4 erroneously shows double pores in the phyllodes. The apical system is clearly tetrabasal in this species. The lectotype of *P. cassiduloides* Gauthier (herein designated) was figured by Gauthier (1889a, pl. 3, figs. 8, 9) and is in the Muséum National d'Histoire Naturelle, Paris. It is figured herein on plate 14, figures 7-9, with an enlarged view of the floscelle of Gauthier's figured paratype on plate 14, figure 10. A drawing of its phyllodes is on text fig. 82. A specimen of *P. toucasanus* (d'Orbigny) from the d'Orbigny Collection is figured on plate 12, figure 6, with a drawing of one of its phyllodes on text figure 83. From the Cotteau Collection at the École des Mines, I have included photographs of two specimens of *P. coquandi* (Cotteau) (pl. 15, figs. 1, 2) and a drawing of a phyllode (text fig. 84).

*Range and distribution.*—Upper Cretaceous (Turonian to Senonian) of Europe and Africa. Lambert and Thiéry (1921, p. 352) give as the range for this genus Valanginian to Senonian. All the pre-Turonian species I have seen have had double-pored phyllodes and should be referred to *Pygorhynchus*.



81

82

83

FIGS. 81-83.—81, *Parapygus nanclasi* (Coquand): Phyllode of ambulacrum I from specimen in Ecole National Supérieure des Mines, Paris, from the Upper Cretaceous (Senonian) at Epagnac (Charente), France,  $\times 10$ . 82, *Parapygus cassiduloides* Gauthier: Phyllode of ambulacrum III of lectotype in Muséum National d'Histoire Naturelle, Paris, from the Upper Cretaceous (Senonian) at Djebel Aidoudi, Tunisia,  $\times 10$ . 83, *Parapygus toucasanus* (d'Orbigny): Phyllode of ambulacrum III of specimen in Ecole National Supérieure des Mines, Paris, from the Upper Cretaceous (Turonian) at Beausset (Var), France,  $\times 15$ .

#### DESCRIPTION OF TYPE SPECIES

#### PARAPYGUS COTTEAUANUS (d'Orbigny)

Plate 14, figures 4-6; text figure 85

*Botriopygus cotteauanus* d'Orbigny, 1856. Pal. franc., Crétacé, vol. 6, pp. 341-342, pl. 932.

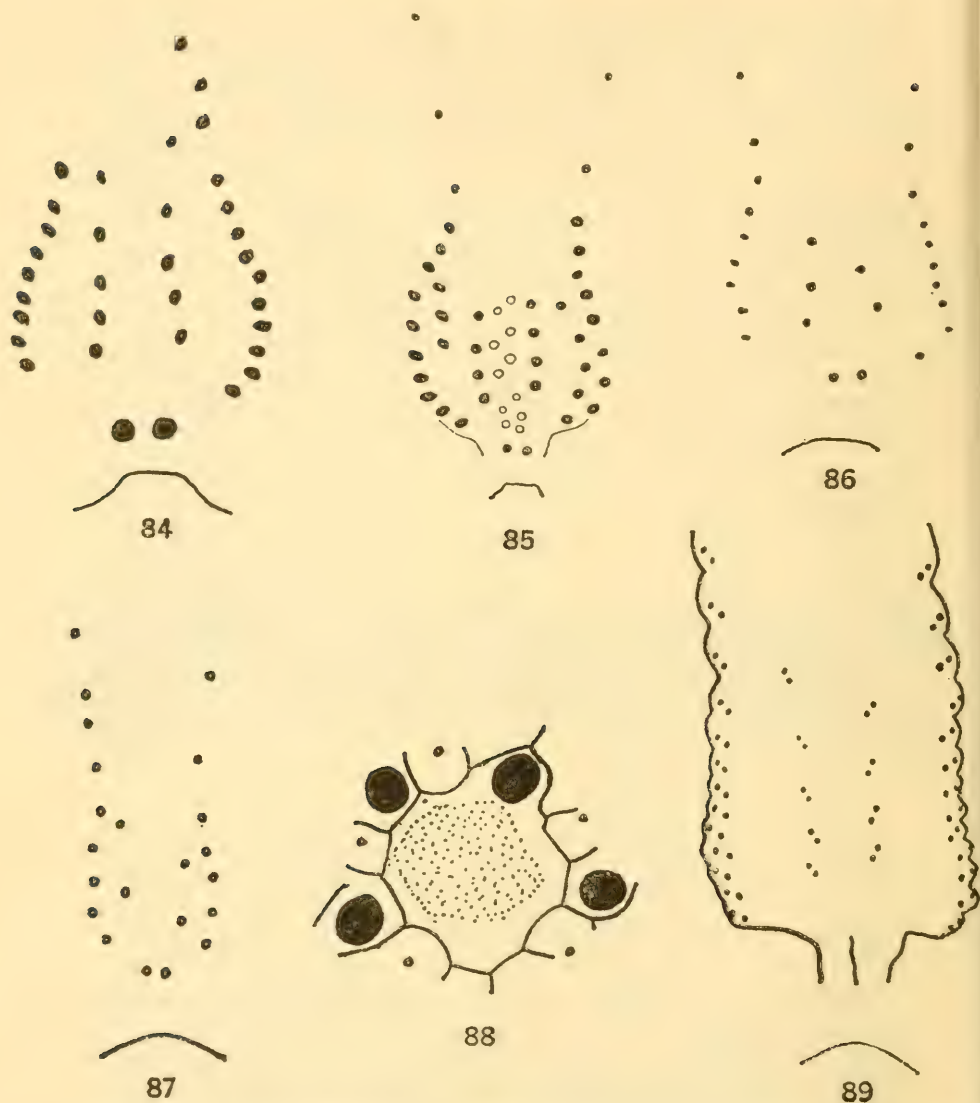
*Material*.—Two specimens studied from the Lambert Collection, Sorbonne, Paris.

*Shape*.—Medium to large (40 to 50 mm. long), oval, inflated adapically, flattened adorally.

*Apical system*.—Anteriorly eccentric, tetrabasal, posterior genital plates separated by genital 2.

*Ambulacra*.—Well-developed petals with wide interporiferous zones, one-third wider than poriferous zones, petals with slight tendency to close distally; anterior petals extend to near margin, posterior petals between one-half and two-thirds distance to margin; pores conjugate with outer pore of pore pair slitlike, inner pore round.





FIGS. 84-89.—84, *Parapygus coquandi* (Cotteau): Phylloide of ambulacrum II of specimen in Ecole National Supérieure des Mines, Paris, from the Upper Cretaceous (Senonian) at Djelfa, Algeria,  $\times 15$ . 85, *Parapygus cotteauanus* (d'Orbigny): Phylloide of ambulacrum IV of specimen in Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Turonian) at Les Martigues, France,  $\times 5$ . 86, *Parapygus longior* (Cotteau and Gauthier): Phylloide of ambulacrum I of specimen in Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Senonian) at Aftab, Persia,  $\times 15$ . 87, *Arnaudaster gauthieri* Lambert: Phylloide of ambulacrum III of the holotype in the Lambert Collection, Sorbonne, Paris, from the Cretaceous (Cenomanian), *Mantelliceras mantelli* (Sowerby) zone, near Fumel, Aquitaine, France,  $\times 15$ . 88, 89, *Pygorhynchus columbianus* (Cooke): 88, Apical system of paratype USNM 108696, from the Lower Cretaceous (Late Albian) at Rancheria Valley, 10 km. north of Fonseca, Dept. Magdalena, Colombia,  $\times 5$ ; 89, phylloide of ambulacrum I of holotype, from same locality,  $\times 15$ .



*Periproct*.—Marginal, higher than wide.

*Peristome*.—Regular, pentagonal, anterior, in faint groove.

*Floscelle*.—Bourrelets strongly developed (pl. 14, fig. 6), vertical sides, curving convexly into peristome; phyllodes (text fig. 85) single pored; in half area of ambulacrum III arranged with 9 pores in each outer series, 4 in each inner; in other ambulacra pores of outer series arranged in 2 columns with a total of 12 to 14 pores in each outer series, 4 in each inner; buccal pores present.

*Tuberculation*.—Naked zone along midzone of interambulacrum 5 on adoral side.

*Occurrence*.—Upper Cretaceous (Turonian) at Martigues (Bouches-du-Rhone), and Castelet (Var), France.

*Location of type specimen*.—Probably in d'Orbigny Collection, Muséum National d'Histoire Naturelle, Paris.

*Remarks*.—d'Orbigny's figure does not show the naked area in interambulacrum 5. I believe its absence in his figure is an error on the part of the artist, as this naked zone is very evident in specimens I have studied (see pl. 14, fig. 5).

#### Synonym of PARAPYGUS

*Pseudocatopygus* Cotteau and Gauthier, 1895. Mission sci. Perse, éch. foss., p. 62. Type species, *Pseudocatopygus longior* Cotteau and Gauthier, by subsequent designation, Kier, herein.

#### DESCRIPTION OF TYPE SPECIES

##### PARAPYGUS LONGIOR (Cotteau and Gauthier)

Plate 15, figures 3, 4; text figure 86

*Pseudocatopygus longior* Cotteau and Gauthier, 1895. Mission sci. Perse, éch. foss., p. 64, pl. 10, figs. 1-4.

*Material*.—Four topotypic specimens studied in the Lambert Collection, Sorbonne, Paris.

*Shape*.—Medium size, 24 to 29 mm. long, elongate, inflated, greatest width and height posterior to center.

*Apical system*.—Anterior, four genital pores, probably tetrabasal.

*Ambulacra*.—Petals short, equal length, wide, interporiferous zones almost twice width of poriferous zones; poriferous zones of same petal of unequal length, petals closing distally; pore pairs conjugate, outer pore transversely elongate, inner round.

*Periproct*.—Marginal, longitudinally elongate, slight groove adoral of opening.

*Peristome*.—Anterior, pentagonal, slightly depressed.

*Floscllc.*—Bourrelets moderately developed; phyllodes (text fig. 86) single pored, broad, 7 or 8 pores in each outer series, 2 or 3 in each inner series; buccal pores present.

*Tuberculation.*—Narrow, naked, granular zone adorally in inter-ambulacrum 5.

*Occurrence.*—Upper Cretaceous (Senonian) of Aftab, Persia.

*Location of type.*—Probably in Cotteau Collection, École des Mines, Paris.

*Remarks.*—This species was considered by Lambert and Thiéry (1921, p. 352) and Mortensen (1948, p. 143) congeneric with *Parapygus cotteauanus*. I agree with their conclusions, as both species have the same elongate, inflated shape with greatest width posterior to center, and similar short petals with anteriorly very eccentric apical system. Their phyllodes differ slightly, with fewer pores in *P. longior*.

#### Synonym of PARAPYGUS

*Rostropygus* Szőrényi, 1955. Geol. Hung., p. 66. Type species by original designation, *Rostropygus annae* Szőrényi.

*Remarks.*—I have not seen any specimens of the type species, but Dr. Szőrényi very kindly sent me some photographs and a cast of the holotype. Szőrényi distinguishes her genus by its projecting posterior margin. However, the type species is so similar in petal arrangement and shape to *Parapygus* that this character does not seem of sufficient importance to warrant the maintenance of a separate genus for it.

#### Genus ARNAUDASTER Lambert

*Arnaudaster* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 82, p. 32. All previous workers including Lambert and Thiéry (1921, p. 353), Mortensen (1948, p. 157), and Neave (1939, p. 301) have attributed this genus to Lambert (1920a). However, he mentioned the genus in 1918 with a diagnosis in a footnote, and that date must be considered the date of its publication. Type species, *Arnaudaster gauthieri* Lambert by subsequent designation, Lambert, (1920a, p. 152).

#### GENERIC DESCRIPTION

Medium size, elongate, subcylindrical, apical system anterior, apparently tetrabasal but sutures not clear on holotype, four genital pores; petals well developed, broad, closing distally, with unequal poriferous zones, pores conjugate, single pores in ambulacral plates beyond petals; periproct marginal, longitudinal; peristome anterior,

subpentagonal; bourrelets present; phyllodes slightly broadened, single pored, approximately six pores in each outer series in each half-ambulacrum, two in each inner; buccal pores.

*Comparison with other genera.*—*Arnaudaster* is very similar to *Parapygus* and perhaps should be considered a synonym of it. It differs only in having a more cylindrical shape, and more unequal poriferous zones in the same petal.

*Remarks.*—Only one species of this genus is known. Cooke (1955, p. 96) attributed a Late Albian species (his *Arnaudaster colombianus*) to this genus, but I do not believe that it is congeneric with *A. gauthieri*. The most important difference between the two species is that the phyllodes in Cooke's species are double pored (text fig. 89) with many pore pairs, and with no buccal pores, whereas in *A. gauthieri* they are single pored with few pores, and with buccal pores. Furthermore, in Cooke's species the poriferous zones are approximately equal in length, but in *A. gauthieri* they are very unequal. On his paratype (USNM 108696) the apical system is well preserved and is definitely tetrabasal (text fig. 88). This species probably should be referred to *Pygorhynchus*.

*Range and distribution.*—Cretaceous (Cenomanian). France.

#### DESCRIPTION OF TYPE SPECIES

#### ARNAUDASTER GAUTHIERI Lambert

Plate 15, figures 5-7; text figure 87

*Arnaudaster gauthieri* Lambert, 1920a. Mém. Soc. Acad. Aube, vol. 84, pp. 152-153, pl. I, figs. 1-4.

*Material.*—The holotype and only known specimen was studied in the Lambert Collection. This specimen is well preserved although the sutures in the apical system are not clear.

*Shape.*—Medium size, holotype 28 mm. long; subcylindrical, with rounded margins and straight sides. Greatest height posterior, adoral surface flat.

*Apical system.*—Anterior, four genital pores, madreporite large, pierced with many pores, apparently tetrabasal from position of genital plates, although sutures not clear.

*Ambulacra.*—Petals well developed, broad, closing distally. Interporiferous zones almost twice width of poriferous zone; pores conjugate, outer pore elongated obliquely, inner round or slightly elongated. Poriferous zones unequal, posterior zones of petals II and IV longer with 8 to 10 more pore pairs than anterior zones; in petal

III right poriferous zone with 3 or 4 more pore pairs than left; in petals V and I outer poriferous zones with 9 more pore pairs than inner poriferous zones.

*Periproct*.—Marginal, longitudinal, in slight groove.

*Peristome*.—Anterior, subpentagonal.

*Floscelle*.—Bourrelets slightly developed. Phyllodes (text fig. 87) broadened, single pored, with few pores: six or seven in each outer series, two in each inner series of a half-ambulacrum. Buccal pores present.

*Occurrence*.—Cretaceous (Cenomanian), *Mantelliceras mantelli* (Sowerby) zone; near Fumel, Aquitaine, France.

*Location of type specimen*.—Holotype in Lambert Collection, Sorbonne, Paris.

#### Genus ECHINOLAMPAS Gray

*Echinolampas* Gray, 1825. Ann. Philos., vol. 26, p. 429. Type species by subsequent designation, Pomel (1883, p. 62), *Echinus oviformis* Gmelin.

Synonyms: ? *Aplolampas* Lambert; *Craterolampas* Cotteau; *Cylindrolampas* Lambert; *Cypholampas* Lambert; *Euechinolampas* Pomel; *Heteroclypeus* Cotteau; *Hypsoclypus* Pomel; *Hypsoheteroclypeus* Szörényi; *Isolampas* Lambert; *Libyolampas* Lambert; *Macrolampas* Lambert; *Merolampas* Pomel; *Miolampas* Pomel; *Oeidolampas* Lambert; *Palaeolampas* Bell; *Planilampas* Mortensen; *Politolampas* Lambert; *Progonolampas* Bittner; *Psammolampas* Lambert; *Scutolampas* Lambert; *Sphelatus* Pomel.

#### GENERIC DESCRIPTION

Medium to large forms, often with high test, elongate to circular, apical system monobasal, petals moderately developed, sometimes lanceolate, open, or closing distally, poriferous zones usually unequal, interporiferous zones wide, single pores in ambulacral plates beyond petals; periproct inframarginal, transverse, peristome transverse, pentagonal; bourrelets well developed; phyllodes single pored, usually moderately developed, with from two to three series of pores in each half-ambulacrum; buccal pores present; tubercles adorally same size as adapically; usually narrow naked granular zone in interambulacrum 5.

*Comparison with other genera*.—*Echinolampas* differs from *Plesiolampas* in having a transverse instead of longitudinal periproct, and from *Parapygus* by having less developed petals with narrower poriferous zones, and usually a larger, wider test. It differs from *Rhyncholampas* in having an inframarginal periproct, narrower petals, and a less developed floscelle.



*Remarks.*—Species of this genus are very abundant in the Tertiary. According to Roman (1955, p. 689) there are more than 285 species. Because of this large number of species several attempts have been made to divide the genus into subgenera or sections. Lambert and Thiéry (1921, pp. 377-384; 1924, p. 385) divide the genus into eight sections, but these sections are distinguished on variable characters as shown by the fact that different specimens of one species have been referred to more than one section (see Kier, 1957, p. 848). Mortensen (1948, p. 272) "lumped" many of these sections but still maintained two subgenera and created a new third. It is my opinion that all these sections and subgenera are based on characters too variable to be of generic distinction. The shape in *Echinolampas* is so variable that, for example, in *Echinolampas fraasi* De Loriol, specimens of different sizes are so different in shape that Checchia-Rispoli referred them to three different species, when in reality only one species was represented as shown by a study of a large number of specimens from one locality (Kier, 1957, p. 852). All these sections and subgenera are herein considered synonyms of *Echinolampas*. I have included figures of the phyllodes of several of the type species of these former subgenera.

Santos' (1958, p. 11) *Anisopetalus oliveirai* from the Miocene of Brazil is an *Echinolampas*. I have studied the holotype and another specimen. This species is an *Echinolampas* as shown by its infra-marginal, transverse periproct.

*Range and distribution.*—Eocene—Recent of worldwide distribution.

#### DESCRIPTION OF TYPE SPECIES

#### **ECHINOLAMPAS OVIFORMIS (Gmelin)**

Plate 30, figures 1-4; text figure 90

*Echinus oviformis* Gmelin, 1789. Linn. Syst. Nat., ed. 13, p. 3187.

*Material.*—One specimen studied at the Museum of Comparative Zoology, Harvard.

*Shape.*—Large, elongate, greatest width posterior to center, greatest height near center, anterior surface steeply sloping, posterior less steep, somewhat pointed. Adoral surface pulvinate, sunken around peristome.

*Apical system.*—Anterior, monobasal, with minute ocular plates.

*Ambulacra.*—Petals short, petals II, III, and IV extending over one-half distance to margin, petals V and I less than one-half. Poriferous zones unequal, right zone of petal III longer than left, posterior zones of petals II and IV longer than anterior, and outside zones of petals V and I. Interporiferous zones three to four times



width of poriferous zones; petals with tendency to close distally. Pores conjugate, outer pore elongated transversely, inner round.

*Periproct*.—Inframarginal, transverse.

*Peristome*.—Anterior, depressed, pentagonal with steep sides.

*Floscelle*.—Bourrelets well developed, inflated; phyllodes single pored (text fig. 90), in ambulacrum III two series of pores in each half-ambulacrum, 8 to 10 in each outer series, 4 to 6 in each inner; in other ambulacra usually 3 series in each half-ambulacrum with 2 to 4 pores in a middle series; buccal pores present.

*Occurrence*.—Recent of Indian Ocean.

*Location of type specimen*.—Unknown.

*Remarks*.—*Echinolampas oviformis* has been considered by most authors as a junior subjective synonym of *Echinanthus ovatus* Leske. As discussed in more detail on page 226, Leske's figure of his *E. ovatus* is so poor as to make positive identification of it impossible.

#### Synonyms of *ECHINOLAMPAS*

? *Aplolampas* Lambert, 1906. Ann. Soc., Alpes-Maritimes, vol. 20, p. 32. Type species by monotypy, *Echinolampas monteivialis* Schauroth.

*Remarks*.—Lambert actually erected this genus for the specimens that Dames (1878, p. 42) referred to *Echinolampas monteivialis*. In 1918 Lambert made a new species *Aplolampas lonigensis* for these specimens of Dames's and stated that this new species was the type species of his *Aplolampas*. This action is not valid, however, since only the species referred to in the original description can be the type species. *E. monteivialis* must be the type species. Unfortunately, Schauroth's figures of this species are very crude, and it is not possible to know many of its generic or specific characters. It does resemble *Echinolampas*, and *Aplolampas* is herein provisionally considered a synonym of *Echinolampas*. Lambert's *A. lonigensis* has never been well figured either, and its generic affinities are not clear.

*Craterolampas* Cotteau, 1891. Pal. franc., éch. Éocène, vol. 2, p. 186. Type species by original designation, *Echinolampas raulini* Cotteau.

#### DESCRIPTION OF TYPE SPECIES

#### *ECHINOLAMPAS RAULINI* Cotteau

Plate 33, figures 1-4; text figure 94

*Echinolampas raulini* Cotteau, 1863. Congrès Sci. France, Sess. Bordeaux, p. 107.

*Material*.—One topotypic specimen studied from the Faculté des Sciences of the Université de Bordeaux, France. The following description is based on this specimen.



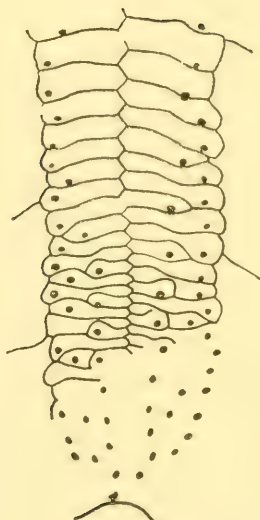
90



91



92



93



94

FIGS. 90-94.—90, *Echinolampas oviformis* (Gmelin): Phyllode of ambulacrum IV of specimen 7249 in the Museum of Comparative Zoology, Harvard, from Pearl Shoal, Indian Ocean (living),  $\times 8$ . 91, *Echinolampas depressa* Gray: Phyllode of ambulacrum II of specimen 8021 in Museum of Comparative Zoology, Harvard, from Key Largo, Florida (living),  $\times 15$ . 92, *Echinolampas crassa* (Bell): Phyllode of ambulacrum V of specimen 2727 in the Museum of Comparative Zoology, Harvard, from Cape Colony off Kromhont, South Africa,  $\times 8$ . 93, *Echinolampas lucae* (Desor): Phyllode of ambulacrum IV of specimen 423 in the Museum of Comparative Zoology, Harvard, from the Miocene of Corsica,  $\times 5$ . 94, *Echinolampas raulini* Cotteau: Phyllode of specimen in Faculté des Sciences de Bordeaux, from the Eocene, Hastings (Landes), France,  $\times 10$  (not all the phyllodal pores were visible on this specimen).

*Shape*.—Large, 65 mm. long, very elongate, narrow, highly inflated with steep sides, posterior margin projecting slightly; adoral surface deeply depressed around peristome.

*Apical system*.—Slightly anterior, monobasal, four genital pores.

*Ambulacra*.—Petals broad, open, extending two-thirds distance from apical system to margin; poriferous zones unequal with 7 more pore pairs in posterior poriferous zones of petals II and IV, 14 more in anterior zones of petals I and V, distal portion of petal III not clear; poriferous zones very narrow; pores conjugate, each pore slightly elongated transversely.

*Periproct*.—Inframarginal, slightly wider than high.

*Peristome*.—Anterior, pentagonal, wider than high, deeply depressed.

*Floscelle*.—Bourrelets well developed, vertical walled, curving convexly into peristome; phyllodes single pored (text fig. 94) with few pores arranged in two series in each half-ambulacrum: six to eight in each outer series, two in each inner. Buccal pores present.

*Occurrence*.—Middle Eocene, Hastings (Landes), France.

*Location of type specimen*.—At the Sorbonne, according to Cotteau.

*Remarks*.—I have not seen Cotteau's type specimens of *E. raulini*, but have studied a specimen identified as *E. raulini* by Castex (1930, p. 31). This specimen is from the same locality as Cotteau's types and is similar in most of its features to Cotteau's figures of *E. raulini*. However, its petals are shorter, and its test is narrower. These differences may reflect inaccuracy on the part of Cotteau's artist, or may be real. Regardless, this specimen is certainly congeneric with Cotteau's specimens.

*Craterolampas* is so similar to *Echinolampas* that it is herein considered a junior subjective synonym. In both genera, the petals are open, with narrow, unequal poriferous zones; the peristome is pentagonal, with well-developed bourrelets and single-pored phyllodes with buccal pores; and the test is large and often highly inflated. *E. raulini* differs from most species of *Echinolampas* in having its peristome depressed, and in having a periproct only slightly wider than high. Cotteau distinguished it further on the grounds that its peristome was rounded and not pentagonal. I suspect that his specimens did not show the peristome clearly, as this portion of the test is not clearly drawn in his figures. It is definitely pentagonal in Castex's specimen.

Cotteau considered *E. raulini* closely related to *Conoclypus* and concluded that until it was known whether or not jaws occurred in

this species, it could not be known whether this species was closely related to *Echinolampas* or *Conoclypus*. The presence of phyllodes with buccal pores is evidence that jaws did not occur in *E. raulini*.

*Cylindrolampas* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 55, p. 44.

Type species by original designation, *Echinolampas subcylindricus* Desor.

*Cypholampas* Lambert, 1906. Ann. Soc. Lett., Sci., Arts Alpes-Maritimes, vol. 20, p. 33. Type species by original designation, *Clypeaster stelliferus* Lamarck.

*Euechinolampas* Pomel, 1887. Pal. de l'Algeria, p. 127. Type species herein designated *Echinolampas florescens* Pomel.

*Heteroclypeus* Cotteau, 1891. Pal. franc., éch. Éocène, vol. 2, p. 104. Type species by original designation, *Galerites semiglobus* Lamarck.

*Hypsoclypus* Pomel, 1869. Revue des échinodermes, p. 25. Type species herein designated, *Conoclypus lucae* Desor (= *Conoclypus plagiosomus* L. Agassiz).

#### DESCRIPTION OF TYPE SPECIES

##### **ECHINOLAMPAS LUCAE (Desor)**

Plate 30, figure 5; plate 31, figure 1; plate 32, figure 1; text figure 93

*Conoclypus lucae* Desor in Agassiz and Desor, 1847. Ann. Sci. Nat., ser. 3, Zool., vol. 7, p. 168.

*Material*.—One specimen studied from the Lambert Collection at the Sorbonne, and one from the Museum of Comparative Zoology, Harvard.

*Shape*.—Very large, subcircular, domed, adoral surface flat.

*Apical system*.—Monobasal, with small ocular plates.

*Ambulacra*.—Petals long, extending almost to margin, broad, with interporiferous zones four times width of poriferous zones; pores slightly conjugate, outer pore of pore pair slightly elongated transversely, inner round; poriferous zones of unequal length: more pore pairs in right zone of petal III, posterior zones of petals II and IV, and outer zones of petals V and I; petals straight, with no tendency to close distally.

*Periproct*.—Inframarginal, transverse.

*Peristome*.—Slightly anterior, transverse, pentagonal.

*Floscelle*.—Bourrelets well developed, inflated, vertically sided, phyllodes (text fig. 93) well developed, slight broadening near peristome; single pored, with many pores arranged in three series in each half-ambulacrum: 10 to 12 in each outer series, 6 to 8 in each of two inner series.

*Occurrence*.—Miocene of Mediterranean countries.

*Location of type specimen*.—In Michelin Collection, probably at École des Mines, Paris.



*Remarks.*—All authors have considered *C. plagiosomus* as the type species of *Hypsoclypus*. However, *C. plagiosomus* is a junior subjective synonym of *C. lucae*. L. Agassiz's (1840a, p. 5) *Conoclypus plagiosomus* is a nomen nudum. Agassiz and Desor (1847, p. 168) described two species, *Conoclypus plagiosomus* and *Conoclypus lucae*, and later Desor (1858, p. 322) made *C. plagiosomus* a junior subjective synonym of *C. lucae*. Many authors have stated that *C. plagiosomus* is the type species of *Hypsoclypus*, but their action has not been a valid designation of *C. lucae*, even though it is a synonym, because none of these authors stated in the same publication that *C. plagiosomus* = *C. lucae*.

Mortensen (1948, p. 316) is mistaken when he states that there are no true phyllodes in *Hypsoclypus*, and that the pores are arranged in single series. The phyllodes are very well developed, being widened near the peristome, and with three series of pores in each half-ambulacrum.

This genus cannot be distinguished from *Echinolampas*. Apparently the only character that served to distinguish *Hypsoclypus*, other than the mistaken idea that it had no phyllodes, was its great size, but a young specimen of the type species would have to be referred to *Echinolampas*.

*Hypsoheteroclypeus* Szörényi, 1953. Geol. Hung., ser. Palaeont., vol. 23, p. 76.

Type species by original designation, *Hypsoclypus doma* Pomel.

*Remarks.*—Szörényi established her *Hypsoheteroclypeus* as a new name for *Hypsoclypus* and *Heteroclypeus*, believing that her action would reduce the confusion resulting in the use of these latter two names. However, since both *Hypsoclypus* and *Heteroclypeus* are older names, her *Hypsoheteroclypeus* cannot stand. *Echinolampas doma* is very similar to the *Echinolampas lucae* (Desor) (= *E. plagiosomus* (L. Agassiz) and certainly congeneric with it.

*Isolampas* Lambert, 1906. Ann. Soc., Alpes-Maritimes, vol. 20, p. 33. Type species by original designation, *Echinolampas goujoni* Pomel.

*Libyolampas* Lambert, 1914. Revue paleozool., vol. 18, p. 112. Type species by original designation, *Echinolampas africanus* De Loriol.

*Macrolampas* Lambert, 1906. Ann. Soc., Alpes-Maritimes, vol. 20, p. 33. Type species by original designation, *Clypeaster hemisphericus* Lamarck. Drawing of a phyllode is included (text fig. 97).

*Merolampas* Pomel, 1883. Class. méth., p. 63. Type species, *Echinolampas mattsensis* Quenstedt, by subsequent designation, Lambert (1918, p. 44).

*Miolampas* Pomel, 1883. Class. méth., p. 62. Type species, *Echinolampas depressa* Gray, by subsequent designation, Lambert (1918, p. 44). A photograph of the adapical surface (pl. 31, fig. 2) and a drawing of a phyllode (text fig. 91) is included.

- Oeidolampas* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 55, p. 44. Type species by original designation, *Echinolampas ataxensis* Cotteau.
- Palaeolampas* Bell, 1880. Proc. Zool. Soc. London, vol. 18, p. 43. Type species by monotypy, *Palaeolampas crassa* Bell. A photograph of the adapical surface and floscelle (pl. 31, figs. 3, 4) and a drawing of a phyllode (text figure 92) are included.
- Planilampas* Mortensen, 1948. Monogr. Ech., vol. 4, pt. 1, p. 297. Type species by original designation, *Echinolampas sternopetala* Agassiz and Clark.
- Politolampas* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 55, p. 45. Type species by original designation, *Clypeaster politus* Lamarck.
- Progonolampas* Bittner, 1892. Sitzungsab. Kais. Akad. Wiss., Math.-Nat. Klasse, vol. 101, Bd. 3, p. 357. Type species by original designation, *Progonolampas novae-hollandiae* Bittner, 1892 (= *Echinolampas posterocrassus* Gregory, 1890).

## DESCRIPTION OF TYPE SPECIES

**ECHINOLAMPAS POSTEROCRASSUS** Gregory

Plate 32, figures 5-7; text figure 96

*Echinolampas posterocrassus* Gregory, 1890. Geol. Mag., n.s., dec. 3, vol. 7, No. 11, p. 483, pl. 13, figs. 4-6.

*Material*.—Four specimens studied from the U. S. National Museum collections.

*Shape*.—Medium size, oval, pointed posterior extremity, inflated adapical surface, rounded adoral surface with depressed peristome, inflated interambulacrum 5; greatest width and height posterior to center.

*Apical system*.—Anterior monobasal, with large, slightly inflated madreporite.

*Ambulacra*.—Petals slightly developed, poriferous zones of unequal length with approximately 4 more pore pairs in right poriferous zone than in left in petal III, 8 to 10 more in posterior zones of petals II and IV, and 10 in outer poriferous zones of petals II and V; pores conjugate, outer pore slightly elongated transversely, inner pore round.

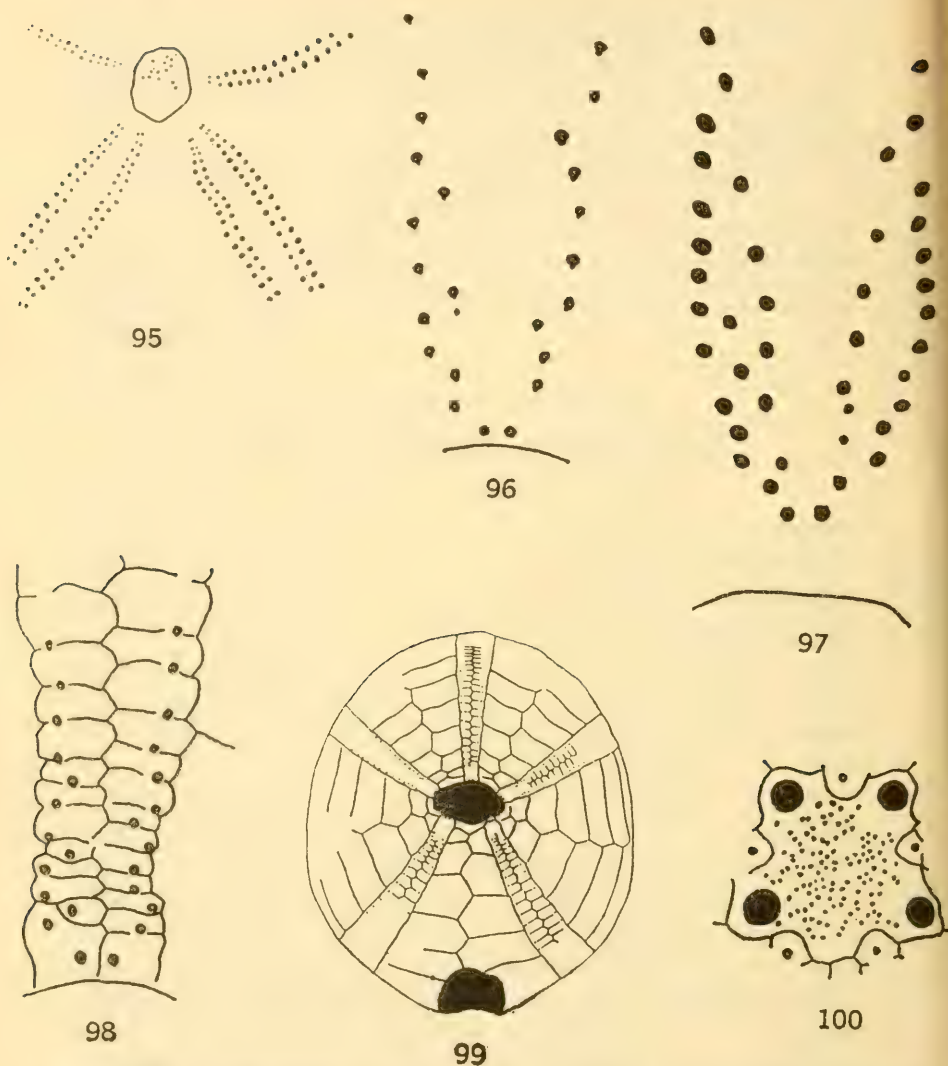
*Periproct*.—Inframarginal, transverse, adoral side of opening slightly depressed.

*Peristome*.—Anterior, very depressed, pentagonal.

*Floscelle*.—Bourrelets slightly developed, phyllodes single pored (text fig. 96) slightly developed, with eight pores in each outer series, two in each inner, little crowding of pores; buccal pores present.

*Occurrence*.—Upper Eocene of South Australia.

*Location of type specimen*.—British Museum (Natural History).



FIGS. 95-100.—95, *Echinolampas lehoni* (Cotteau): Portion of adapical area of holotype in Musée Royal d'Histoire Naturelle de Belgique, Brussels, from the Eocene at Saint-Gilles, Belgium, approximately  $\times 6$ . 96, *Echinolampas posterocrassus* Gregory: Phyllode of ambulacrum II of USNM 634000, from the Upper Eocene (Aldingian) at Aldinga, South Australia,  $\times 15$ . 97, *Echinolampas hemisphericus* Lamarck: Phyllode of ambulacrum IV of specimen in Museum of Comparative Zoology, Harvard,  $\times 8$ . 98-100, *Plesiolampas* sp., cf. *P. ovalis* Duncan and Sladen: 98, Phyllode of ambulacrum IV of specimen C4359 in the collections of the University of California, from the Paleocene Ranikot beds, Baluchistan,  $\times 15$ ; 99, adoral plate arrangement of same specimen,  $\times 2$ ; 100, apical system of specimen C4361, from same locality,  $\times 15$ .

*Remarks.*—Lambert and Thiéry (1924, p. 387) considered *Progonolampas* as a subgenus of *Echinolampas* characterized as having simple round, nonconjugate pores. However, the pores are not simple (see pl. 32, fig. 5), but are strongly conjugate, with the outer pores slightly elongated transversely. I agree with Mortensen (1948, p. 278) in considering *Progonolampas* as a synonym of *Echinolampas*.

Bittner evidently had not seen Gregory's paper when he described his species *P. novae-hollandiae*. His species is identical with Gregory's *E. posterocrassus*. Gregory's paper was published just two years before Bittner's.

*Psammolampas* Lambert, 1913. Mém. Soc. Pal. Suisse, vol. 39, p. 136. Type species by original designation, *Echinolampas scutiformis* Desmoulins.

*Scutolampas* Lambert, 1906. Ann. Soc., Alpes-Maritimes, vol. 20, p. 33. Type species by original designation, *Conoclypus plagiosomus* L. Agassiz (= *Echinolampas lucae* (Desor)).

*Sphelatus* Pomel, 1883. Class. méth., p. 54. Type species by monotypy, *Caratomus lehoni* Cotteau.

#### DESCRIPTION OF TYPE SPECIES

#### ECHINOLAMPAS LEHONI (Cotteau)

Plate 32, figures 2-4; text figure 95

*Caratomus lehoni* Cotteau, 1880. Mém. Acad. Roy. Sci., Lett. et Beaux-arts de Belgique, vol. 43, p. 25, pl. 2, figs. 14-20.

*Material.*—I studied the holotype, which is the only specimen known of this species.

*Shape.*—Very small, 9.5 mm. long, marginal outline circular except for slight posterior prolongation; highly inflated with steep but smoothly curved sides, slight oblique posterior truncation; adoral surface smoothly depressed around peristome.

*Apical system.*—Anterior, very large relative to size of test, elongate, monobasal, madreporite elevated, pierced with approximately 13 pores, no genital pores.

*Ambulacra.*—Ambulacrum III not petaloid, petals II and IV short, curving anteriorly (text fig. 95), no petaloid pores in anterior poriferous zones, 14 pore pairs in petaloid portions of posterior poriferous zones; petals V and I extending halfway to margin, with slight tendency to close distally, interporiferous wider than poriferous, tapering slightly distally; poriferous zones unequal, right zone of petal I with two more pore pairs than left, left zone of petal V with two more pore pairs than right; pores conjugate, outer pores slightly elongated transversely, inner circular.



*Periproct*.—Inframarginal, large, transverse.

*Peristome*.—Anterior, large, transverse, subpentagonal.

*Floscelle*.—Bourrelets forming a flange around peristome. Phylloides not broadened, with slight crowding of pores, single pored; buccal pores.

*Tuberculation*.—Tubercles large, of approximately same size ad-orally as adapically, scrobicular ring large, with approximately 15 scrobicular tubercles in each ring; boss small, perforate.

*Occurrence*.—Eocene at Saint-Gilles, Belgium.

*Location of type specimen*.—Musée Royal d'Histoire Naturelle de Belgique, Brussels, Belgium.

*Remarks*.—If Cotteau's description and figures of this species had been correct, and if they had been based on adult specimens, then Pomel would have been correct in erecting a new genus for it. The lack of a petal in ambulacrum III, absence of petaloid pores in the anterior poriferous zones of petals II and IV, the high globular test, and the five genital plates are characters of sufficient importance to distinguish generically this species from any other species known. However, these characters either do not occur in this species, or, in my opinion, are immature characters which would not be found on an adult of this species. Cotteau states in his description that the apical system has four genital plates, but in his figure shows five. Pomel did not see the specimen, but stated, presumably after studying Cotteau's figures, that there were five genital plates. I was able to study the holotype, and only known specimen of this species, under high magnification, and without doubt the apical system is monobasal. I believe that all the other characters that would generically distinguish this species are immature and that this species is an *Echinolampas*, and probably an *Echinolampas affinis* (Goldfuss). One would expect a young specimen of an *Echinolampas* to look exactly like the holotype of *E. lehoni*. The following features of *E. lehoni* are also found in the young of *Echinolampas fraasi* De Loriol as described by Kier (1957, p. 849): The most obvious and striking evidence of immaturity is the lack of genital pores. Cotteau in his description says that the genital plates are perforated but in his figures shows them to be imperforate. I examined the apical system with high magnification both dry and immersed in alcohol, and there are definitely no genital pores. In *E. fraasi* genital pores do not occur on any specimens less than 14 mm. long (the holotype of *E. lehoni* is 9.5 mm. long). In *E. lehoni* as in the young of *E. fraasi* there are very few madreporic pores, and the apical system

is very large relative to the size of the test. The test of *E. lehoni* is very high as is also the young test of *E. fraasi*. Further characters in *E. lehoni* also found in the young of *E. fraasi* are the large subpentagonal peristome, larger periproct, large tubercles, and slight crowding of pores in the phyllodes. The absence of petaloid pores in ambulacrum III and the anterior poriferous zones of petals II and IV also reflects the immaturity of the specimen of *E. lehoni*. In an adult of *Echinolampas* there are usually less pore pairs in petal III and the anterior poriferous zones of petals II and IV. Since any inequality in the number of pore pairs must date back to the first appearance of the pore pairs, there must be a period in the early growth of an *Echinolampas* when there are no pore pairs in petal III, and none or few in the anterior poriferous zones of petals II and IV, after they have already begun to be formed in the posterior poriferous zones of petals II and IV. Such is the case in *E. lehoni*, and such was the case in *E. fraasi*.

Specimens of *Echinolampas affinis* are very common at the same locality where the holotype of *E. lehoni* was collected. It is probable that *E. lehoni* is a young *E. affinis*, as both have the same shaped petals with petals II and IV curving anteriorly, and similarly shaped periproct and peristome. I have seen only a few specimens of *E. affinis*, however, and hesitate to make *E. lehoni* definitely a synonym of *E. affinis* without having studied a growth series.

#### Genus PLESIOLAMPAS Duncan and Sladen

*Plesiolampas* Duncan and Sladen, 1882. Pal. Indica, ser. 14, vol. 1, p. 9. Type species by monotypy, *Plesiolampas elongata* Duncan and Sladen. Synonym: *Oriolampas* Munier-Chalmas.

#### GENERIC DESCRIPTION

Medium to large size, elongate, low, apical system monobasal; petals long, open, narrow poriferous zones, of unequal length in same petal; single pores in ambulacral plates beyond petals; periproct inframarginal, longitudinal; peristome transverse; bourrelets well developed, phyllodes single pored, with slight crowding of pores; buccal pores present; tubercles on adoral surface approximately same size as on adapical.

*Comparison with other genera.*—This genus is most similar to *Echinolampas* having similar petals, bourrelets, phyllodes, and tuberculation, but differing in having a longitudinal periproct.

*Remarks.*—I was unable to study any specimens of the type species

but saw a well-preserved specimen of *P. placenta* Duncan and Sladen borrowed from the Exeter Museum, England, 13 specimens of *Plesiolampas* sp. cf. *P. ovalis* Duncan and Sladen, from the University of California, and many specimens of *P. curriæ* Kier and *P. auraduensis* Kier in the Sedgwick Museum, Cambridge, England. Photographs are included of *P. placenta* (pl. 34, figs. 1-3) and drawings of the phyllodes (text fig. 98), apical system (text fig. 100), and adoral plate structure (text fig. 99) in *P.* sp. cf. *P. ovalis*. As discussed in Kier (1957, p. 855) there has been some controversy over whether the tubercles were perforate crenulate or imperforate non-crenulate in this genus, but there is no doubt that they are perforate crenulate in all the species.

*Range and distribution.*—Paleocene to Eocene of India, Africa, Europe, and Tasmania.

#### Synonym of PLESIOLAMPAS

*Oriolampas* Munier-Chalmas, August 1882. Bull. Soc. Géol. France, ser. 3, vol. 10, p. 369; pro *Neolampas* Munier-Chalmas (1879) non *Neolampas* A. Agassiz (1869). Type species by monotypy, *Amblypygus michelini* Cotteau (in Cotteau and Leymerie, 1856).

*Remarks.*—I have not seen any specimens of the type species, but there is no doubt from a study of Cotteau's figures that this species is congeneric with the type species of *Plesiolampas*. Munier-Chalmas did not know of Duncan and Sladen's *Plesiolampas* when he published his *Oriolampas* later in the same year.

#### Genus CONOLAMPAS A. Agassiz

*Conolampas* A. Agassiz, 1883. Mem. Mus. Comp. Zool., vol. 10, No. 1, p. 48. Type species by monotypy, *Conoclypus sigsbei* A. Agassiz.

#### GENERIC DESCRIPTION

Large, high, circular outline, adoral surface flat; apical system monobasal, petals long, straight, with narrow poriferous zones, pores slightly conjugate, ambulacral plates beyond petals single pored; periproct inframarginal, transverse; peristome pentagonal; bourrelets well developed, phyllodes single pored with many pores arranged in three series in each half-ambulacrum; buccal pores.

*Comparison with other genera.*—*Conolampas* is very similar to *Echinolampas* and is perhaps a synonym of it. It differs only in having narrower, straighter poriferous zones in its petals.

*Range.*—Recent.



## DESCRIPTION OF TYPE SPECIES

## CONOLAMPAS SIGSBEI (A. Agassiz)

Plate 34, figures 8, 9

*Conoclypus sigsbei* A. Agassiz, 1878. Bull. Mus. Comp. Zool., vol. 5, p. 190, pls. 1, 2.

*Material*.—Many specimens studied at the Museum of Comparative Zoology, Harvard, and one in the U. S. National Museum.

*Shape*.—Very large, circular in marginal outline, very high, adoral surface flat.

*Apical system*.—Central, monobasal.

*Ambulacra*.—Petals long, straight, extending almost to margin, broad with interporiferous zones three to four times width of poriferous zones, petals with no tendency to close distally; poriferous zones narrow with pore equal, round, not conjugate or just slightly conjugate; zones of unequal length, more pore pairs in right zone of petal III, posterior zones of petals II and IV, and outer zones of V and I.

*Periproct*.—Inframarginal, transverse.

*Peristome*.—Central to slightly posterior, pentagonal, transverse.

*Floscelle*.—Bourrelets well developed, inflated, vertically sided; phyllodes single pored, broad, with many pores arranged in three series in each half-ambulacrum.

*Occurrence*.—Living in the West Indies.

*Location of type specimen*.—Museum of Comparative Zoology, Harvard.

## Family FAUJASIDAE Lambert, 1905a

Small to large, often broad, circular to elongate, flat adoral surface; apical system anterior, tetrabasal, or monobasal, four genital pores; periproct supramarginal to inframarginal, often with anal groove; peristome central to anterior; petals equal, broad, closed (except in *Australanthus*), outer pore slitlike, pores strongly conjugate, single pore in all ambulacral plates beyond petals; bourrelets strongly developed; phyllodes usually greatly widened, single pored, with few to many pores, buccal pores present; tubercles larger adorally, naked granular zone in interambulacrum 5.

*Genera*.—*Petalobrissus*, *Stigmatopygus*, *Pygidiolampas*, *Gongrochanus*, *Pygurostoma*, *Lefortia*, *Faujasia*, *Eurypetalum*, *Domechinus*, *Fauraster*, *Hardouinia*, *Australanthus*.

*Range*.—Upper Cretaceous (Cenomanian) to Eocene.



*Remarks.*—The Faujasidae are distinguished by their strongly developed bourrelets, usually broad phyllodes, and broad petals.

#### Genus PETALOBRISSUS Lambert

*Petalobrissus* Lambert, 1916b. Mém. Soc. Acad. Aube, vol. 80, p. 82. Type species, *Echinobrissus setifensis* Cotteau, by original designation.

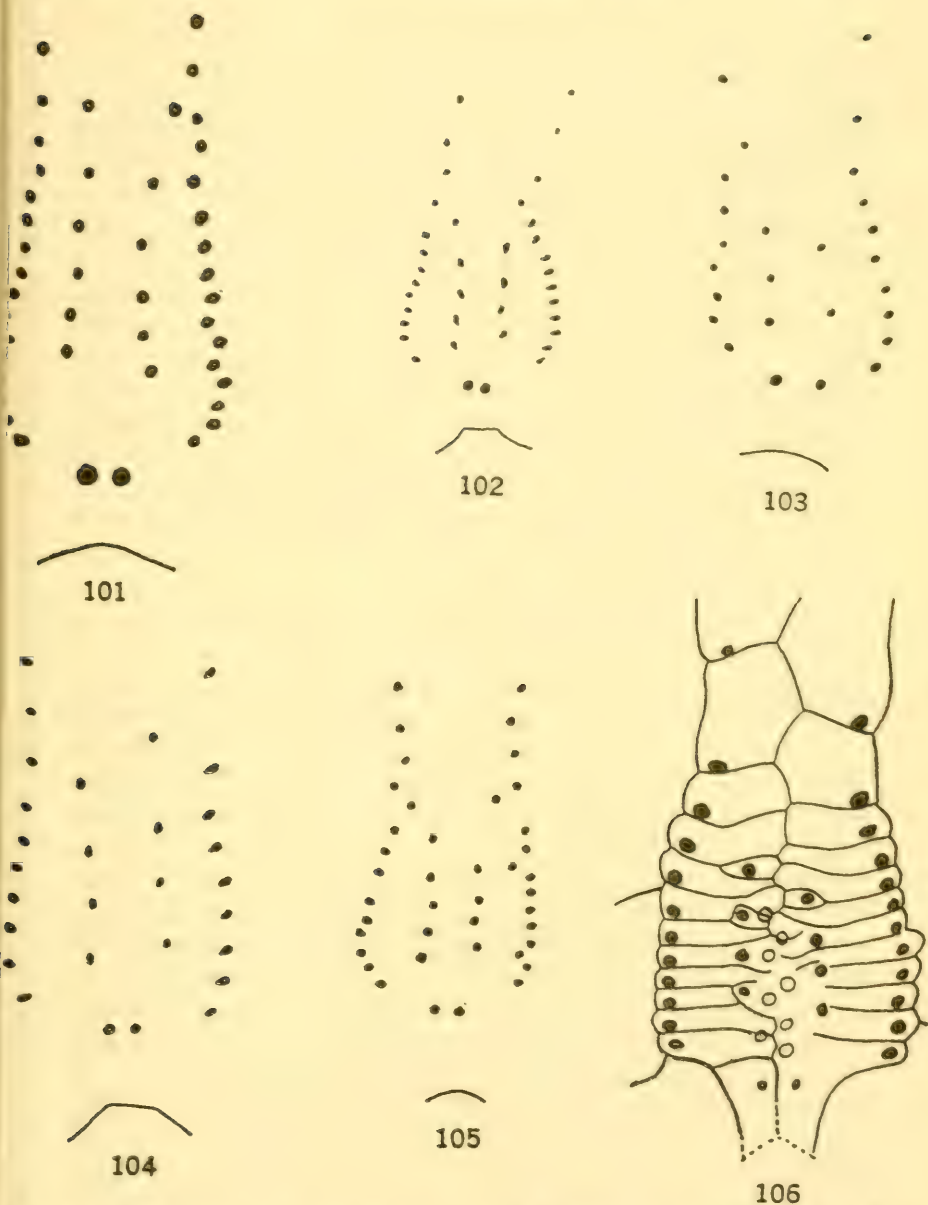
#### GENERIC DESCRIPTION

Small to medium, elongate, somewhat inflated, adoral surface flattened to slightly pulvinate; apical system anterior, tetrabasal, four genital pores; petals broad, equal, poriferous zones of same petal of equal length with conjugate pores; periproct supramarginal to marginal, longitudinal; peristome anterior, pentagonal, wider than high; bourrelets strongly developed, inflated, projecting; phyllodes broad, single pored, with two series of pores in each half-ambulacrum; buccal pores present; narrow naked area in median region in inter-ambulacrum 5 adorally.

*Comparison with other genera.*—*Petalobrissus* is similar to *Phyllobrissus* in the shape of its test, general petal arrangement with equal, broad petals, supramarginal, longitudinal periproct, and tetrabasal apical system. It differs from *Phyllobrissus* in its much more developed bourrelets, single-pored phyllodes, and in having buccal pores. *Petalobrissus* is probably a descendant of *Phyllobrissus* as shown by its more advanced phyllodes, and presence of buccal pores. As would be expected, it occurs later in the Cretaceous than *Phyllobrissus*.

*Petalobrissus* appears to be an ancestor of *Hardouinia*. It is very similar to some of the more primitive species of *Hardouinia* and has very similar phyllodes. It differs in having an anterior peristome and less prominent bourrelets.

*Remarks.*—Lambert considered this genus as only a subgenus of *Clypeopygus*. Although somewhat similar in general appearance, they are generically distinct. *Clypeopygus* is a more primitive form, with double-pored phyllodes and lacking buccal pores. It occurs earlier in the Cretaceous, although Lambert and Thiéry (1921, pp. 348-349) list many species that occur in the Turonian and Senonian. I have seen specimens of four of these species, and in every case they have single-pored phyllodes with buccal pores and should be referred to *Petalobrissus* and not *Clypeopygus*. One of these species, *Petalobrissus trigonopygus* (Cotteau) is so similar to the type species of *Petalobrissus* that it could almost be considered conspecific with it. I have included a photograph (pl. 15, fig. 10) and a drawing of a phyllode (text fig. 101) of this species. *Petalobrissus djelfensis*



FIGS. 101-106.—101, *Petalobrius trigonopygus* (Cotteau): Phyllode of ambulacrum V of specimen in Muséum national d'Histoire Naturelle, Paris, from the Upper Cretaceous (Santonian) at Ain Aourou, Algeria,  $\times 15$ . 102, *Petalobrius djelfensis* (Gauthier): Phyllode of ambulacrum II of holotype in the Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Santonian) at Djelfa, Algeria,  $\times 10$ . 103, *Petalobrius ammonis* Fourtau: Phyllode of ambulacrum IV of paratype (No. 25410) in Geological Museum, Cairo, Egypt, from the Upper Cretaceous (Turonian) at head of Wadi Tarfa, Egypt,  $\times 15$ . 104, *Petalobrius lefebvrei* (Fourtau): Phyllode of ambulacrum II of holotype (No. 25408) in Geological Museum, Cairo, Egypt, from the Upper Cretaceous (Turonian) at Abu Roash, West Cairo, Egypt,  $\times 15$ . 105, *Petalobrius neltneri* (Lambert): Phyllode of ambulacrum II of holotype in the Lambert Collection, Sorbonne, Paris, from the Cretaceous (Cenomanian), at Msouma, 24 km. east of J'Adouz, Algeria,  $\times 10$ . 106, *Petalobrius eubensis* (Weisbord): Phyllode of ambulacrum III of USNM 131265, from the Upper Cretaceous (Senonian) at Rio Seco, Medina County, Tex.,  $\times 10$ .

(Gauthier), another post-Cenomanian species that Lambert and Thiéry refer to *Clypeopygus*, is certainly a *Petalobrissus*. I have studied the holotype in the Lambert Collection at the Sorbonne and include photographs (pl. 16, figs. 1-3) of the specimen and a drawing (text fig. 102) of one of its phyllodes. Its petals are very similar to *P. setifensis* and it has single-pored phyllodes with buccal pores. It is probable that none of the post-Cenomanian species that Lambert and Thiéry refer to *Clypeopygus* belong to that genus.

Lambert's (1931, p. 31) *Procassidulus neltneri* from the Cenomanian of North Africa is also a *Petalobrissus*. I studied the holotype in the Lambert Collection at the Sorbonne, and include new photographs (pl. 17, figs. 1-3) of it and a drawing of one of its phyllodes (text fig. 105). Its petals and floscelle are very similar to *Petalobrissus setifensis*, and its supramarginal periproct is similar in location to the periproct in *Petalobrissus djelfensis* (Gauthier). It is easily distinguished from *Procassidulus* (herein considered a synonym of *Rhynchopygus*) by its larger test and much more developed petals and phyllodes.

I have examined many of the Texan specimens referred by Cooke (1953, p. 17) to *Phyllobrissus cubensis* (Weisbord), and if these specimens are conspecific with Weisbord's holotype, this species should be referred to *Petalobrissus*. The phyllodes are single pored (text fig. 106), not double pored as in *Phyllobrissus*, the pores in the petals are more conjugate, the periproct is more supramarginal, and buccal pores are present. I include a drawing (text fig. 107) of the adoral plate arrangement.

Lambert's (1936, p. 5) *Petalobrissus burckhardti* from the Senonian of Mexico looks more like a *Rhynchopygus*. Its small, elongate, flattened test with flush, slightly developed petals and weak phyllodes is typical of *Rhynchopygus* not *Petalobrissus*.

Fourtau's *Echinobrissus ammonis* and *E. lefebvrei* have single-pored phyllodes and should not be referred either to *Echinobrissus* (a junior objective synonym of *Nucleolites*) as done by Fourtau or to *Clitopygus* (= *Nucleolites*) as done by Lambert and Thiéry (1921, p. 346). They are herein referred to *Petalobrissus*. I was able to study the type specimens of these two species, and since Fourtau did not describe many of the important details of them, I have included a redescription and new photographs and drawings below.

*Range and distribution.*—Cretaceous (Cenomanian to Senonian) of North Africa and America.

**PETALOBRISSUS AMMONIS (Fourtau)**

Plate 16, figures 7-9; text figure 103

*Echinobrissus ammonis* Fourtau, 1914. Cat. invertébrés foss. Égypte, terr. Crétacés, échinodermes, p. 49, pl. 4, figs. 8, 9.

*Material*.—I studied Fourtau's figured specimens. The specimen figured in his plate 4, figure 9, is herein designated the lectotype. Both specimens are poorly preserved, being partially silicified and fractured.

*Shape*.—Small, lectotype 20.4 mm. long, paratype 25.5 mm.; elongate, anterior margin smoothly rounded, posterior, blunted to slightly grooved; greatest width posterior to center; adapical surface inflated along median with greatest height at apical system or posterior, sides sloping gently to margin; adorally very depressed.

*Apical system*.—Anterior, apparently tetrabasal but sutures not clear due to silicification; madreporite large, extending posteriorly separating posterior ocular plates, occupying large central area; four genital pores.

*Ambulacra*.—Petals broad, well developed, equal, lanceolate, tendency to close distally, interporiferous zones at greatest width twice width of poriferous zones, tapering distally; poriferous zones with greatest width at midlength, pores conjugate, outer pore elongated, situated oblique to round inner pores.

*Periproct*.—Supramarginal, opening approximately two-thirds distance from apical system to posterior margin, in deep narrow groove extending to margin.

*Peristome*.—Anterior, deeply depressed, pentagonal, slightly higher than wide.

*Floscelle*.—Bourrelets slightly inflated, oblique; phyllodes slightly widened, single pored (text fig. 103) with pores in two series in each half-ambulacrum, approximately eight in each outer series, two or three in each inner; buccal pores present.

*Tuberculation*.—Owing to poor preservation, details of tuberculation not clear.

*Occurrence*.—Upper Cretaceous (Turonian), head of Wadi Tarfa, Egypt.

*Location of type specimen*.—Lectotype and paratype (25410, F 357) in Geological Museum, Cairo, Egypt.



**PETALOBRISSUS LEFEBVREI (Fourtau)**

Plate 16, figures 4-6; text figure 104

*Echinobrissus lefebvrei* Fourtau, 1914. Op. cit., p. 52, pl. 4, fig. 12.

*Material*.—One specimen, the holotype, was studied. Although part of the specimen is fractured, with portions of the test absent, all the important characters are preserved.

*Shape*.—Medium size, holotype 34.2 mm. long; test elongate with smoothly rounded anterior margin, posterior margin with slight truncation at anal groove, sides expanding posteriorly, with greatest width posterior to center; adapical surface inflated, with greatest height posterior to center; adoral surface depressed around peristome.

*Apical system*.—Anterior, tetrabasal, madreporite very large, occupying large central area, extending posteriorly, widely separating posterior ocular plates, other genital plates small.

*Ambulacra*.—Petals broad, equal, medium length, with slight tendency to close distally. Interporiferous zones slightly wider than poriferous, tapering slightly distally. Poriferous zones wide, tapering distally, outer pore very elongated, almost slitlike, situated obliquely distal to slightly elongated inner pore; conjugate. Single pores in plates beyond petals.

*Periproct*.—Supramarginal, between midway and two-thirds distance from apical system to posterior margin, oval longitudinally, in deep, narrow groove, broadening slightly posteriorly, extending to margin.

*Peristome*.—Anterior, depressed, pentagonal, wider than high.

*Floscelle*.—Bourrelets well developed, swollen, vertically sided. Phyllodes slightly widened, single pored (text fig. 104), with pores arranged in two series in each half-ambulacrum, approximately eight in each outer series, four in each inner except in ambulacrum III, where two or three; buccal pores present.

*Tuberculation*.—Tubercles larger adorally, slight naked sternal zone in interambulacrum 5.

*Occurrence*.—Upper Cretaceous (Turonian), Aubu Roash, West Cairo, Egypt.

*Location of type specimen*.—Holotype (25408, F 363) in Geological Museum, Cairo, Egypt.

## DESCRIPTION OF TYPE SPECIES

**PETALOBRISSUS SETIFENSIS (Cotteau)**

Plate 16, figure 10-13; text figures 108, 109

*Echinobrissus setifensis* Cotteau, 1866. Rev. Mag. Zool., ser. 2, vol. 18, pp. 267-268, pl. 14, figs. 13-15.

*Material*.—I studied six specimens in the Muséum National d'Histoire Naturelle, Paris, and one in the U. S. National Museum.

*Shape*.—Small, 20 to 30 mm. long, elongate, subangular in marginal outline, greatest width posterior to center, greatest height anterior; adapical surface inflated, with posterior slightly truncated obliquely; adoral surface flat to slightly pulvinate.

*Apical system*.—Anterior, tetrabasal, four genital pores (text fig. 108), posterior genital plates not in contact.

*Ambulacra*.—Petals well developed, broad, lanceolate equal, closing distally; poriferous and interporiferous zones tapering distally; pores conjugate, outer pore elongated transversely, inner round.

*Periproct*.—On lower edge of slight oblique, posterior truncation, supramarginal with opening slightly visible from above, longitudinal.

*Peristome*.—Anterior, wider than high, pentagonal.

*Floscelle*.—Bourrelets strongly developed, inflated, projecting into peristome; phyllodes (text fig. 109) broad, single pored with two series of pores in each half ambulacrum: 10 to 12 pores in each outer series, 4 or 5 in each inner; buccal pores present.

*Occurrence*.—Upper Cretaceous (Maestrichtian) of Dra-Toumi, Kef Matrek, south of Medjes, Mahdid, Djebel Mzeita, Department of Constantine, Algeria.

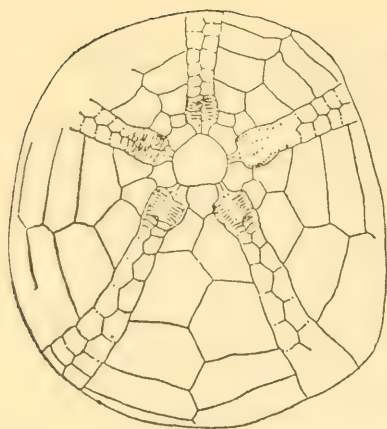
*Location of type specimen*.—According to Cotteau (1866, p. 268) the type specimen is in the Coquand Collection. I do not know where this collection is.

**Genus STIGMATOPYGUS d'Orbigny**

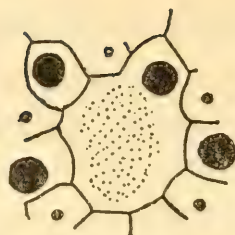
*Stigmatopygus* d'Orbigny, 1856. Pal. franc., Crétacé, vol. 6, p. 331. Type species, *Stigmatopygus galeatus* d'Orbigny by subsequent designation, Lambert and Thiéry (1921, p. 363).

## GENERIC DESCRIPTION

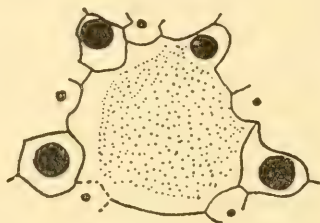
Medium to large size, elongate to broad, inflated adapical surface, flattened adoral; apical system tetrabasal, petals broad, equal, closed, conjugate pores, ambulacral plates beyond petals single pored; periproct supramarginal, longitudinal, high on oblique posterior trunca-



107



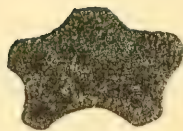
108



110



109



112



111

FIGS. 107-112.—107, *Petalobrissus cubensis* (Weisbord): Adoral plate arrangement of USNM 131265a, from the Upper Cretaceous (Senonian) at Rio Seco, Medina County, Tex.,  $\times 2$ ; 108, 109, *Petalobrissus setifensis* (Cotteau): 108, Apical system of specimen in Muséum National d'Histoire Naturelle, Paris, from the Upper Cretaceous (Maestrichtian) at Kef el Matrek, south of Medjes, Dept. of Constantine, Algeria,  $\times 15$ ; 109, phyllode of ambulacrum I of USNM 131261 from the Upper Cretaceous (Maestrichtian) at El Kantara, Algeria  $\times 15$ ; 110, 111, *Stigmatopodus lamberti* Besairie: 110, Apical system of specimen in collection of General Collignon from the Upper Cretaceous (Campanian) at Gres Andrakaraka, Madagascar,  $\times 10$ ; 111, floscelle of same specimen,  $\times 3$ ; 112, *Pygidiolampas curynota* Clark: Phyllode of holotype (No. 3540) in the Museum of Comparative Zoology, Harvard, probably from the Upper Cretaceous (Campanian) from the Peedee formation, South Carolina,  $\times 8$ .

tion, deep transverse groove ventral to opening; peristome anterior, pentagonal; bourrelets strongly developed, pointed; phyllodes very broad, deeply depressed between bourrelets, single pored with two series of pores in each half-ambulacrum: approximately 12 in each outer series, 6 in each inner; buccal pores present.

*Comparison with other genera.*—*Stigmatopygus* is quite similar to *Hardouinia*. In both genera the test is large, highly inflated, with supramarginal periproct, broad, closed equal petals, flat adoral surface with very prominent bourrelets, and broad phyllodes. Both genera occur in the Upper Cretaceous and are certainly closely related. *Stigmatopygus* is distinguished from *Hardouinia* by the deep transverse groove ventral to its periproct, and by its anterior peristome.

Apparently these two genera occurred in the same type of environment as is indicated not only by their morphological similarities, but by their occurrence in rocks of strikingly similar lithology. According to personal communication with M. Collignon, specimens of *Stigmatopygus lamberti* Besairie occur in Madagascar in great numbers in a very coarse sandstone that is almost devoid of other fossils. *Hardouinia mortonis* (Michelin) occurs in southeastern United States in rocks of similar lithology. As discussed in detail on page 22, this echinoid probably lived in a high-energy, littoral environment.

*Range.*—Cretaceous (Cenomanian to Senonian) of Africa and Europe.

*Remarks.*—I was unable to find any specimens of the type species, *S. galeatus*, in any of the Paris museums. According to d'Orbigny (1856, p. 333) the holotype, presumably the only specimen known, was in the D'Archiac Collection. According to Lambert and Jeannet (1928, p. 102), the D'Archiac Collection is not intact, as he sold many of his specimens.

I have been able to study many specimens of *Stigmatopygus lamberti* Besairie, a species very similar to *S. galeatus* and certainly congeneric with it. I include a description and figures of this species as a substitute for a description of the type species.

#### STIGMATOPYGUS LAMBERTI Besairie

Plate 20, figures 5-8; text figures 110, 111

*Stigmatopygus lamberti* Besairie, 1930. Bull. Soc. Hist. Nat. Toulouse, vol. 60, p. 572, pl. 13, figs. 1-8.

*Material.*—General Collignon very kindly lent me 103 specimens from his personal collection. Two specimens were studied in the Muséum National d'Histoire Naturelle, Paris.



*Shape*.—Medium to large, larger specimens 65 mm. long, elongate to broad, width less than length; adapical surface highly inflated with greatest height posterior to center, gently sloping anterior surface, steeply sloping, slightly truncated posterior surface; adoral surface flat.

*Apical system*.—Slightly anterior, tetrabasal (text fig. 110), genital 2 extending posteriorly separating posterior genital plates; four genital pores.

*Ambulacra*.—Petals broad, equal, closed, with broad tapering interporiferous and poriferous zones; conjugate pores, outer pore slitlike, inner slightly elongated transversely.

*Periproct*.—Supramarginal, high on oblique posterior truncation, between one-half and two-thirds distance from apical system and posterior margin; longitudinal, forming notch in overhanging dorsal surface. Deep, broad depression ventral to periproct, extending laterally across test.

*Peristome*.—Anterior, pentagonal, wider than high, flush with adoral surface.

*Floscelle*.—Bourrelets strongly developed, jutting into peristome, toothlike. Phyllodes (text fig. 111) broad, deeply depressed between bourrelets, single pored with two series of pores in each half ambulacrum, approximately 12 pores in each outer series, 5 or 6 in each inner. Buccal pores widely separated from edge of peristome. Sphaeridia in two series in middle of ambulacrum.

*Tuberculation*.—Tubercles considerably larger on adoral surface than on adapical; midzone of interambulacrum 5 with no tubercles adorally.

*Occurrence*.—Upper Cretaceous (Upper Campanian), Andraraka sandstone, near Andrafiavelo (Maintirano), Madagascar.

*Location of type specimen*.—Unknown.

*Remarks*.—I suspect that the periproct is not keyhole or flask shaped in *S. galeatus* as described and figured by d'Orbigny. Forbes (1846, pl. 19, fig. 1b—plates published in 1856) showed a similarly shaped periproct in *Stigmatopygus elatus* (herein considered *Gongrochanus herschelianus*), but as first pointed out by Stoliczka (1873, p. 27) and confirmed by my own examination of the holotype (see pl. 19, fig. 6), the periproct is round to oval, but has a broad, transverse depression ventral to it which, when combined with it, gives the appearance of a flask-shaped periproct. The periproct in *S. lamberti* is very similar in appearance. Probably in d'Orbigny's specimen of *S. galeatus* the depressed area ventral to the periproct was partially

filled with matrix giving the impression that it was part of the periproct. In many of the specimens of *S. lamberti* I studied, the periproct appeared to be flask shaped for the same reason.

#### Genus PYGIDIOLAMPAS Clark

*Pygidiolampas* Clark, 1923. Bull. Mus. Comp. Zool., vol. 65, p. 345. Type species by original designation, *Pygidiolampas curynota* Clark.

#### GENERIC DESCRIPTION

Medium length, broad, circular except for pointed posterior margin, adapical surface inflated, adoral flat or slightly depressed; apical system tetrabasal; petals broad, equal, closed, with very wide interporiferous zones, tapering distally, pores conjugate, outer pore slit-like, ambulacral plates beyond petals single pored; periproct inframarginal, very small, longitudinal; peristome central, pentagonal; bourrelets strongly developed, toothlike; phyllodes single pored, greatly broadened, with pores arranged in two series: outer series in arc with approximately 10 pores in each series, inner series with few pores, all pores widely separated from peristome; buccal pores present.

*Comparison with other genera.*—This genus is very similar to *Hardouinia*. Both genera have broad, equal closed petals, high, circular tests, and both have strikingly similar floscelles with strongly developed, toothlike bourrelets and broad phyllodes with the pores arranged in arelike fashion around the peristome. The genera are distinguished from each other by the location of the periproct. In *Hardouinia* the periproct is supramarginal, whereas in *Pygidiolampas* it is inframarginal.

Lambert and Thiéry (1925, p. 587) considered *Pygidiolampas* a synonym of *Pygurus* (their *Echinopygus*). However, they did not see any specimens of *Pygidiolampas*, but based their decision on Clark's inadequate illustrations. *Pygidiolampas* is quite distinct from *Pygurus* as shown by the great difference in their phyllodes. The phyllodes in *Pygurus* are double pored and the pores are not arranged in arcs as in *Pygidiolampas*, and there are no buccal pores, whereas they are present in *Pygidiolampas*. Clark considered his genus similar to *Echinolampas*, but in the petals in *Echinolampas* the outer pore of a pore pair is not slitlike as in *Pygidiolampas*, the petals are never as wide, the phyllodes do not have their pores arranged in arcs, and the bourrelets are never toothlike.

*Remarks.*—Morton's (1834) *Clypeaster geometricus* was referred by Cooke (1953, p. 14) to *Pygurostoma* and later (1955, p. 98)

questionably referred to *Faujasia*. There is no doubt that this species is congeneric and probably conspecific with *Pygidiolampas eurynota*. They are identical in all characters. If more and better specimens of the species were available, I am certain they would prove to be conspecific. Specimens of the two species have been collected in rock of approximately the same age. *Pygidiolampas eurynota* was supposed to have been collected in the Miocene at the Grove Plantation, Cooper River, near Charleston, S. C. However, the matrix in the holotype is a glauconitic sandstone, whereas the other echinoids collected at the Grove Plantation are preserved in a yellow marl. According to Dr. Norman Sohl, who is the authority on this region, this glauconitic sandstone is identical to that found in the Campanian Peedee formation. The specimen of *Pygidiolampas geometricus* was collected at what was reported to be the Marshalltown formation at the north side of the Chesapeake and Delaware Canal, 2,000 feet east of the railroad bridge. Later workers (Groot, Organist, and Richards, 1954) have considered this locality to be either Navesink or Mt. Laurel. According to Stephenson et al. (1942) and confirmed by Dr. Sohl in personal communication, these two formations are equivalent in age to the Peedee formation.

*Range and distribution*.—Upper Cretaceous (Campanian) of South Carolina and Delaware.

#### DESCRIPTION OF TYPE SPECIES

#### PYGIDIOLAMPAS EURYNOTA Clark

Plate 20, figures 2-4; text figure 112

*Pygidiolampas eurynota* Clark, 1923. Bull. Mus. Comp. Zool., vol. 65, pp. 346-348, text fig. 2.

*Material*.—The holotype and only known specimen was studied.

*Shape*.—Medium size, holotype 46 mm. long, marginal outline circular except for pointed posterior; adapical surface inflated, adoral flat.

*Apical system*.—Central to slightly anterior, tetrabasal.

*Ambulacra*.—Petals broad, equal, extending over two-thirds distance to margin, closed, with very wide interporiferous zones tapering distally; poriferous zones wide with outer pore of pore pair slitlike, inner slightly elongated transversely, pores conjugate.

*Periproct*.—Inframarginal, very small, longitudinal.

*Peristome*.—Central, pentagonal.

*Floscelle*.—Bourrelets strongly developed, projecting into peristome.



toothlike, phyllodes single pored, broad, deeply depressed between bourrelets, with pores arranged in two series (text fig. 112) in each half-ambulacrum: outer series arclike with approximately 10 pores, inner series linear with 3 pores: buccal pores and phyllodal pores widely separated from edge of peristome.

*Occurrence*.—Upper Cretaceous (Campanian) probably from the Peedee formation, South Carolina.

*Location of type specimen*.—Holotype (No. 3540) in the Museum of Comparative Zoology, Harvard.

*Remarks*.—The peristome region (pl. 20, fig. 3) in the holotype is misshapen near the posterior ambulacrum, and the phyllode in ambulacrum I is absent. This distortion is not due to poor preservation but is a pathological abnormality.

#### GONGROCHANUS Kier, new name

pro *Cyrtoma* M'Clelland, 1840. *Calcutta Journ. Nat. Hist.*, vol. 1, No. 2, p. 185; non *Cyrtoma* Meigen, 1824, a dipter. Type species, *Cyrtoma herscheliana* M'Clelland.

#### GENERIC DESCRIPTION

Large, broad, adapical surface highly inflated with posterior region obliquely truncated; adoral surface flat to slightly depressed; apical system tetrabasal, three genital pores in the type species; petals broad, approximately equal, in type species petal III is slightly longer than the others; interporiferous zones broad, tapering distally, pore pairs conjugate, outer pore slitlike, inner round to slightly elongated transversely, ambulacral plates beyond petals single pored; periproct supramarginal, longitudinal, in notch with groove extending ventrally to margin; peristome central, wider than high; bourrelets strongly developed, jutting into peristome, toothlike; phyllodes very broad, single pored, with many pores arranged in each half-ambulacrum in two regular series with many pores irregularly scattered between these two series; prominent bulge occurring in median area of each ambulacrum; buccal pores near edge of peristome.

*Comparison with other genera*.—This genus is very similar to *Stigmatopygus*. Both Lambert and Thiéry (1921, p. 304) and Mortensen (1948, p. 217) considered it a synonym of the latter. It is similar in its general shape, petal arrangement, and position of periproct, but its floscelle is sufficiently different to warrant generic distinction. In the phyllodes in *Gongrochanus herschelianus* there are almost 70 pores in a half-ambulacrum, arranged in two regular series with



many pores scattered irregularly between these two series, whereas in *S. lamberti* and *S. galeatus* there are one-quarter as many pores and all of them are in two regular series. An even more striking feature in *Gongrochanus herschelianus* is the prominent bulge in the median area of each phyllode. This feature is not present on any of the species of *Stigmatopygus*, or as far as I know, in any other echinoid.

*Range and distribution.*—Upper Cretaceous (Senonian) of India.

#### DESCRIPTION OF TYPE SPECIES

##### GONGROCHANUS HERSCHELIANUS (M'Clelland)

Plate 19, figures 4-6; plate 20, figure 1; text figure 118

*Cyrtoma herscheliana* M'Clelland, 1840. Calcutta Journ. Nat. Hist., vol. 1, No. 2, pp. 185-187, pl. 5, figs. 1-3.

*Material.*—I studied the three syntypes of Forbes' (1846, p. 162, pl. 19, fig. 1, published in 1856) *Nucleolites elatus*, a junior subjective synonym of *Gongrochanus herschelianus*. These specimens are in the British Museum (Natural History). Specimen No. E 42324 is herein designated the lectotype of Forbes' species. His figures are a reconstruction, as none of the three specimens shows all the characters depicted on one of his figures. All the specimens are poorly preserved, being badly weathered and fractured.

*Shape.*—Large, elongate to broad, highly inflated, with flat or slightly depressed adoral surface.

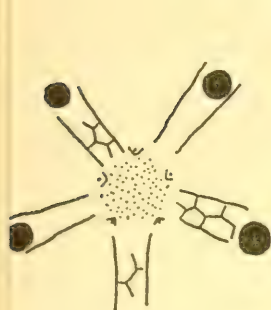
*Apical system.*—Slightly posterior to slightly anterior to center, tetrabasal, according to Stoliczka (1873, p. 28) only three genital pores, no pore in genital 2.

*Ambulacra.*—Petals broad, closed, petal III longer than others. Interporiferous zones broad, tapering distally; pores conjugate, outer pore slitlike, inner round to slightly elongated transversely.

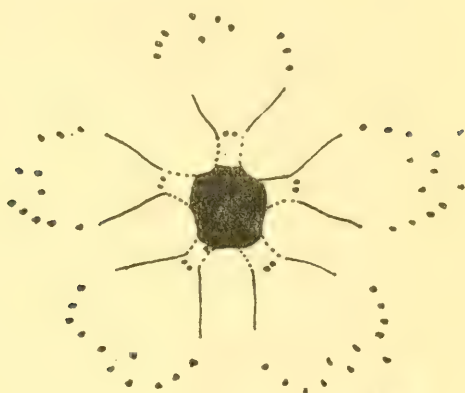
*Periproct.*—Supramarginal, in groove forming notch, extending to posterior margin, opening longitudinal to circular.

*Peristome.*—Central, wider than high.

*Floscelle.*—Bourrelets strongly developed, jutting into peristome, toothlike. Phyllodes very broad, with many single pores arranged regularly in two series in each half-ambulacrum with many pores scattered irregularly between these series: approximately 26 pores in each outer series, 15 in each inner (text fig. 118) and 26 irregularly scattered between; pores widely separated from edge of peri-



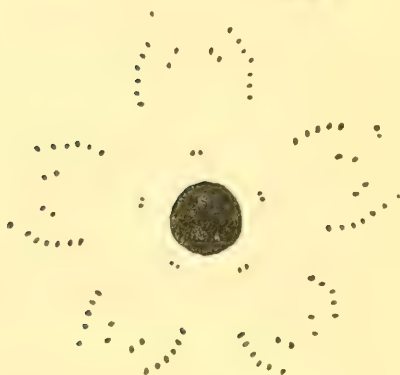
113



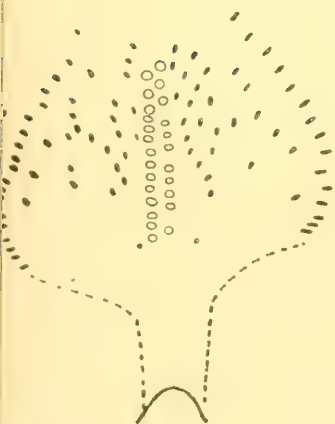
114



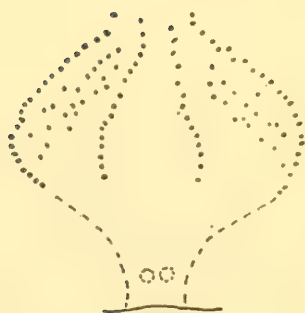
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118

FIGS. 113-118.—113, 114, *Faujasia apicalis* (Desor): 113, Apical system of USNM 131272, from the Upper Cretaceous (Maestrichtian), Albert Canal, Vroenhoven, Belgium,  $\times 15$  (note position of genital pores in interambulacra; most sutures not visible); 114, phylloides of same specimen,  $\times 6$ . 115, 116, *Lefortia delgadoi* (Loriol): 115, Apical system of lectotype in Servicos Geologicos de Portugal, Lisbon, from the Upper Cretaceous (Senonian) at Azonhaga de Pinhal de Laura (Mira), Portugal,  $\times 8$ ; 116, phylloides of same specimen,  $\times 6$ . 117, *Pygurostoma morgani* Cotteau and Gauthier: Phylloide of ambulacrum V of specimen in the Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Senonian) at Aftab (Louristan), Persia,  $\times 6$ . 118, *Gongrochannus herschelianus* (McClelland): Phylloide of ambulacrum V of paratype No. E42326 in the British Museum (Natural History), from the Upper Cretaceous (Senonian) of southern India.

stome. Buccal pores near peristome. Prominent bulge occurring longitudinally in median area of each phyllode (pl. 20, fig. 1).

*Tuberculation*.—Tubercles on adoral surface much larger than those on adapical; no tubercles in median area of interambulacrum 5 adorally.

*Occurrence*.—Upper Cretaceous (Senonian), Arriallor group, in southern India.

*Location of type specimen*.—Unknown.

*Remarks*.—Forbes (1846), d'Orbigny (1856, p. 333), and Stoliczka (1873) apparently were unaware of M'Clelland's description of *Gongrochanus herschelianus* when they described or referred to *Gongrochanus elatus*, a species which is certainly conspecific with it. According to Stoliczka, the species is very variable, with smaller specimens being more elongate and lower than larger specimens. It was this variability that caused M'Clelland to erect seven species for specimens which probably belong to the same species (see Das-Gupta, 1921, p. 297).

Mortensen (1948, text fig. 195) shows a posterior view of *Gongrochanus herschelianus* which he cites as being copied from d'Orbigny (1856, pl. 929). d'Orbigny in his text says that the species is figured on his plate 929, but this is an error, for *Pygorhynchus obovatus* is figured there. Mortensen's figure must have been copied from Forbes (1846, pl. 19, fig. 1b, published in 1856).

#### Genus PYGUROSTOMA Cotteau and Gauthier

*Pygurostoma* Cotteau and Gauthier, 1895. Mission scientifique en Perse par J. de Morgan, vol. 3, pt. 2, Paléontologie, p. 51. Type species by monotypy, *Pygurostoma morgani* Cotteau and Gauthier.

#### GENERIC DESCRIPTION

Medium to large, elongate, low; apical system anterior, tetrabasal; periproct marginal to inframarginal, longitudinal; peristome transverse pentagonal; petals broad, equal, closed, conjugate pores; ambulacral plates beyond petals single pored; bourrelets well developed; phyllodes broad, single pored, with many pores, buccal pores small, widely separated from edge of peristome.

*Comparison with other genera*.—*Pygurostoma* is quite distinct from the other genera in the family Faujasidae. Its floscelle, however, is very similar to that found in *Gongrochanus*, having many single pores and strongly developed bourrelets, but *Pygurostoma*

differs in having a marginal to inframarginal periproct, and a low, very elongate test.

*Range and distribution.*—Upper Cretaceous (Senonian) of Persia and Guatemala.

#### DESCRIPTION OF TYPE SPECIES

##### **PYGUROSTOMA MORGANI** Cotteau and Gauthier

Plate 19, figures 1-3; text figure 117

*Pygurostoma morgani* Cotteau and Gauthier, 1895. Mission scientifique en Perse par J. de Morgan, vol. 3, pt. 2, Paléontologie, p. 52, pl. 8, figs. 1-5.

*Material.*—One topotypic specimen studied from the Lambert Collection, at the Sorbonne, and one in the Muséum National d'Histoire Naturelle, Paris.

*Shape.*—Medium to large (65 mm. long), elongate, with slightly pointed posterior margin, low, greatest width posterior to center, greatest height at center; adoral surface slightly depressed.

*Apical system.*—Slightly anterior, tetrabasal, four genital pores.

*Ambulacra.*—Petals broad, equal, flush with test, extending two-thirds distance to margin, with broad interporiferous zones; petal III open, all other petals closing distally; poriferous zones broad, tapering distally, pores conjugate, outer pore slitlike, inner pore slightly elongated transversely, zones of equal length.

*Periproct.*—Marginal to inframarginal, longitudinal, very narrow.

*Peristome.*—Anterior, pentagonal, wider than high.

*Floscelle.*—Well developed (see pl. 19, fig. 3). Bourrelets strongly inflated, toothlike; phyllodes very broad (text fig. 117), deeply depressed between bourrelets, single pored with many pores: approximately 15 in each outer series, 25 scattered irregularly in inner area in each half-ambulacrum. Buccal pores small, widely separated from peristome edge. Sphaeridia in two rows in middle of ambulacrum.

*Occurrence.*—Upper Cretaceous (Senonian) of Persia.

*Location of type specimen.*—Not found by this author.

*Remarks.*—This species has always been considered as having a monobasal apical system. On the specimen I studied in the Muséum National d'Histoire Naturelle only a portion of the system was visible, but without any doubt it was tetrabasal.

#### Genus **LEFORTIA** Cossman

*Lefortia* Cossman, 1901 (January). Rev. crit. paléozool., vol. 5, p. 58. Type species by monotypy, *Pomelia delgadoi* De Loriol.



## GENERIC DESCRIPTION

Small, low, broad, flat adoral surface; apical system tetrabasal, with genital pores in normal position in genital plates; petals long, broad, equal, closing distally; ambulacral plates beyond petals single pored; periproct marginal, small, longitudinal; peristome anterior, circular with height equal to width; bourrelets strongly developed, toothlike, phyllodes broad, single pored, few pores arranged in two series in each half-ambulacrum, pores widely separated from peristome; buccal pores on edge of peristome.

*Comparison with other genera.*—Lambert and Thiéry (1921, p. 363) considered *Lefortia* a subgenus of *Procassidulus*. *L. delgadoi* resembles the type species of *Procassidulus* (= *Rhynchopygus*), *R. lapiscancræ* (Leske), in having a flattened adoral surface, well-developed bourrelets, broad, single-pored phyllodes, and a tetrabasal apical system. It differs from *R. lapiscancræ* in having a marginal instead of supramarginal periproct, a larger test, and more pronounced petals.

*Lefortia* resembles *Eurypetalum* but differs in having a marginal, longitudinal periproct as opposed to an inframarginal, transverse periproct. *Faujasia* differs from *Lefortia* in having its genital pores in the interambulacra, monobasal apical system, and an inframarginal, transverse periproct. In *Domechinus* the apical system is monobasal, and the periproct transverse rather than longitudinal.

*Remarks.*—Cooke (1953, p. 17) described a new species of *Lefortia*, *L. trojana*, from the Maestrichtian of Mississippi. This species is very similar to the type species, *L. delgadoi*, and is without doubt congeneric. Cooke described its apical system as being monobasal, but I have cleaned the type specimen and found plate sutures around the genital plates showing it to be tetrabasal.

*Range and distribution.*—Cretaceous (Senonian) of Europe, India, Madagascar, and America.

## DESCRIPTION OF TYPE SPECIES

## LEFORTIA DELGADOI (De Loriol)

Plate 18, figures 9-12; text figures 115, 116

*Pomelia delgadoi* De Loriol, 1900. Rev. Suisse Zool., vol. 8, p. 67, pl. 6, figs. 6-8.

*Material.*—De Loriol's four cotypes were studied. The specimen he figured in his plate 6, figure 6, is herein designated the lectotype.

*Shape*.—Small, lectotype 22 mm. long, low, broad, with width almost equal to length, with greatest width and height posterior to center; posterior margin very slightly pointed, anterior smoothly round.

*Apical system*.—Anterior, tetrabasal (text fig. 115), madreporite large, other genital plates small, with left anterior pore eccentric anteriorly.

*Ambulacra*.—Petals strongly developed, broad, equal in length, extending two-thirds distance from apical system to margin, interporiferous zones more than three times width of poriferous zones, petals closing distally; poriferous zones depressed, pores conjugate.

*Periproct*.—Small opening, marginal, longitudinal.

*Peristome*.—Anterior, opening small, round.

*Floscelle*.—Bourrelets strongly developed, pointed; phyllodes (text fig. 116) single pored, broad, with six to seven pores in each outer series, two in each inner; pores widely separated from peristome. Buccal pores minute, on edge of peristome.

*Ornamentation*.—Naked zone in median tract of interambulacrum 5 on adoral surface. Tubercles larger adorally than adapically.

*Occurrence*.—Upper Cretaceous (Senonian) Azinhaga de Pinhal de Laura (Hira), Portugal.

*Location of type specimen*.—Servicos Geologicos de Portugal, Lisbon.

#### Genus FAUJASIA d'Orbigny

*Faujasia* d'Orbigny, 1856, Pal. franc., Crétacé, vol. 6, pp. 290, 314. Type species, *Pygurus apicalis* Desor by subsequent designation, Lambert and Thiéry (1921, p. 273).

#### GENERIC DESCRIPTION

Small to medium, elongate to broad, high or low, blunted anterior margin, pointed posterior, adoral surface flat or depressed; apical system apparently monobasal, four genital pores, with pores in interambulacra, widely separated from apical system by small interambulacral plates; petals short, broad, equal, closed, with broad tapering interporiferous zones, narrow poriferous zones with conjugate pores, outer pores greatly elongated transversely; ambulacral plates beyond petals single pored; periproct inframarginal, small, transverse; peristome anterior, small; bourrelets strongly developed, toothlike, jut-

ting; phyllodes single pored with few pores, arranged in arc distinct from peristome; buccal pores near peristome.

*Comparison with other genera.*—*Faujasia* differs from all other cassiduloids in having its genital pores in the interambulacra. It is most similar to *Eurypetalum*, having similar short, broad, closed petals, a pointed posterior margin, inframarginal periproct, and pointed bourrelets.

*Remarks.*—As pointed out by Cooke (1953, p. 13), the type species should have been *Faujasia faujasii* by virtual tautonymy. However, since *F. apicalis* was designated the type species before any author called attention to the tautonymy, it must remain the type species.

The generic concept of *Faujasia* is herein restricted. In the type species, the apical system and the phyllodes are so distinct from those in all the other species that have been referred to *Faujasia*, except *Faujasia eccentricipora* Lees (1928, p. 661), that it should not be considered congeneric with them. These other species are referred herein to a new genus *Eurypetalum*. In *F. apicalis* the apical system is most unusual in that the genital pores are widely separated from the apical system, occurring deep in the interambulacra, between the petals, with small interambulacral plates occurring between the pores and the apical system. In the other species formerly referred to *Faujasia* the apical system is normal, with the genital pores in the genital plates. Furthermore, in *F. apicalis* the apical system is probably monobasal, whereas it is definitely tetrabasal in the other species. The phyllodes in *F. apicalis* have very few pores, and they are arranged in an arc, whereas in the other species formerly referred to *Faujasia* there are many more pores, and they are arranged in two series in each half-ambulacrum.

Evidently, the apical system in *F. eccentricipora* is very similar to that in *F. apicalis*. The pores are widely separated from the rest of the apical system, although Lees says that they are in the genital plates. Evidently, he just presumed that the genital plates extended out between the petals and included the genital pores, for he states in his description that he was unable to see any plate sutures. Unfortunately, he does not figure the phyllodes, and without this information his species can be referred only tentatively to *Faujasia*.

*Range and distribution.*—Upper Cretaceous (Maestrichtian) of western Europe and probably Arabia.

## DESCRIPTION OF TYPE SPECIES

**FAUJASIA APICALIS** (Desor)

Plate 17, figures 9-11; text figures 113, 114

*Pygurus apicalis* Desor, in Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, Zool., vol. 7, p. 162.

*Material*.—Five specimens studied in the U. S. National Museum.

*Shape*.—Small (25 mm. long), subangular marginal outline, blunted anteriorly, pointed posteriorly, greatest width posterior to center. Adapically highly inflated, apex pointed, with greatest height anterior, at apical system; adorally flat.

*Apical system*.—Anterior, four genital pores, with pores located in interambulacra, separated from apical system by small interambulacral plates (text fig. 113); apparently monobasal, madreporic pores occurring in whole central area; ocular plates very small.

*Ambulacra*.—Petals inconspicuous, flush, equal, closed, short, extending approximately one-half distance from apical system to margin; interporiferous zones broad, tapering, greatest width one-third distance from apical system to end of petal; poriferous zones narrow, with conjugate pores, outer pore greatly elongated transversely, inner pore round to slightly elongated.

*Periproct*.—Supramarginal, very small, transverse.

*Peristome*.—Anterior, small, slightly higher than wide, pentagonal.

*Floscelle*.—Bourrelets strongly developed, toothlike, jutting into peristome (pl. 17, fig. 11); phyllodes broad, deeply depressed between bourrelets, single pored, in arclike arrangement with few pores, 10 to 12 in whole phyllode (text fig. 114) pores widely separated from peristome; buccal pores near edge of peristome.

*Ornamentation*.—Tubercles on adoral surface considerably larger than those on adapical; adorally, no large tubercles in median tract in interambulacrum 5.

*Occurrence*.—Upper Cretaceous (Maestrichtian) of Belgium and Holland.

*Location of type specimen*.—Unknown; according to Desor, in the collection of the Marquis of Northampton. Sherborn (1940, p. 35) says that the collection of the second Marquis of Northampton (S. J. A. Compton) was transferred from Castle Ashby in 1878 to Northampton Museum.



**EURYPETALUM Kier, new genus**

*Type species.*—*Echinolampas faujasii* Desmoulins.

## GENERIC DESCRIPTION

Test medium size, elongate, blunted anterior margin, pointed posterior, adapical surface moderately inflated, adoral surface flattened; apical system tetrabasal, anterior, four genital pores in genital plates; petals broad, conspicuous, closed, equal, conjugate pores, outer pore greatly elongated transversely, ambulacral plates beyond petals single pored; periproct inframarginal, small, transverse; peristome anterior, pentagonal, width approximately equal to height; bourrelets well developed, rounded; phyllodes broad, single pored, with two series of pores in each half-ambulacrum.

*Comparison with other genera.*—This genus is similar to *Faujasia* in its shape and petal arrangement, but is distinguished from that genus by its apical system, which is tetrabasal, with the genital pores in normal position in the genital plates, whereas in *Faujasia* the apical system is probably monobasal, with its genital pores not in the apical system, but in the interambulacra. If d'Orbigny's (1856, pl. 923, fig. 2) figure of the phyllodes in *Eurypetalum faujasii* is correct, this genus can be further distinguished by the more numerous pores in its phyllodes than in *F. apicalis*. *Eurypetalum* is somewhat similar to *Lefortia*, but differs in having a transverse, inframarginal periproct as opposed to the marginal, longitudinal periproct in *Lefortia*. It differs from *Domacchinus* in that this latter genus has a monobasal apical system and a much higher test.

*Range and distribution.*—Upper Cretaceous (Senonian) of France, Belgium, and Holland.

## DESCRIPTION OF TYPE SPECIES

**EURYPETALUM FAUJASII (Desmoulins)**

Plate 17, figures 7, 8

*Echinolampas faujasii* Desmoulins, 1837. *Études sur les éch.*, p. 346.

*Material.*—Two specimens (one topotypic) studied in the Museum of Comparative Zoology at Harvard, and one in the d'Orbigny Collection at the Muséum National d'Histoire Naturelle, Paris. All the specimens are internal casts.

*Shape.*—Medium size, adults 35 to 40 mm. long, elongate, with gently curved anterior margin, pointed posterior, greatest width

posterior to center; adapical surface low, adoral flattened but slightly depressed around peristome.

*Apical system*.—Sutures visible on specimen studied in d'Orbigny Collection, definitely tetrabasal, with four genital pores in genital plates, genital 2 extending posteriorly, separating posterior genital plates.

*Ambulacra*.—Petals well developed, conspicuous, broad, equal, closed, with broad, tapering interporiferous zones. Pores conjugate, outer pore greatly elongated transversely.

*Periproct*.—Small, inframarginal, transverse.

*Peristome*.—Slightly anterior, pentagonal, width equal to height.

*Floscelle*.—Bourrelets well developed, jutting prominently. Phylloides not visible on any specimens studied but according to d'Orbigny's figure, single pored with two series of pores in each half-ambulacrum. Buccal pores probably present.

*Occurrence*.—Upper Cretaceous (Maestrichtian) of France and Holland.

*Location of type specimen*.—Unknown.

#### DOMECHINUS Kier, new genus

*Type species*.—*Faujasia chelonium* Cooke.

#### GENERIC DESCRIPTION

Medium size, elongate, blunted anterior margin, pointed posterior, adapical surface inflated, adoral flat; apical system monobasal with four genital pores; petals conspicuous, broad, equal, closed, conjugate pores, ambulacral plates single pored beyond petals; periproct marginal or slightly inframarginal, small, transverse; peristome slightly anterior, small, pentagonal; bourrelets strongly developed, toothlike; phylloides single pored, two series of pores in each half-ambulacrum, six to eight pores in each outer series, only one or two pores in each inner; buccal pores present.

*Comparison with other genera*.—*Domechinus* is quite similar to *Faujasia*, *Lefortia*, and *Eurypetalum*. Its monobasal apical system distinguishes it from *Lefortia* and *Eurypetalum*. Furthermore, in *Lefortia* the periproct is longitudinal, whereas in *Domechinus* it is transverse. *Faujasia* differs in its peculiar apical system with the genital pores in the interambulacra.

Cooke (1955, p. 98) referred *Domechinus chelonium* to *Pygurus*.

However, in *Pygurus* the phyllodes are double pored with no buccal pores and the apical system is tetrabasal.

*Range and distribution.*—Upper Cretaceous (Maestrichtian), Texas.

#### DESCRIPTION OF TYPE SPECIES

#### DOMECHINUS CHELONIUM (Cooke)

Plate 18, figures 1-5

*Faujasia chelonium* Cooke, 1953. U. S. Geol. Surv. Prof. Pap. 254-A, p. 14, pl. 4, figs. 11-14.

*Material.*—Only one specimen, the holotype, is known of this species. It is a well-preserved specimen showing the apical system and phyllodes.

*Shape.*—Medium size, holotype 30.5 mm. long, broad, width slightly less than length, anterior margin gently rounded, sides straight, posterior pointed; adapically highly inflated with steep sides; adorally flat to slightly depressed.

*Apical system.*—Slightly anterior, monobasal, with four genital pores.

*Ambulacra.*—Petals conspicuous, broad, equal, closed, interporiferous zones extremely wide, tapering distally, poriferous zones narrow with conjugate pores, outer pore slightly elongated transversely, inner circular.

*Periproct.*—Marginal to inframarginal, transverse, very small.

*Peristome.*—Anterior, small, pentagonal, width equaling height.

*Floscelle.*—Bourrelets strongly developed, pointed (pl. 18, fig. 5), toothlike, jutting into peristome; phyllodes broad, single pored, with pores in two series in each half-ambulacrum: five to seven in each outer series, two in each inner; pores widely separated from peristome; buccal pores on edge of peristome.

*Tuberculation.*—Tubercles very small on both adapical and adoral surfaces; smaller on median tract of interambulacrum 5, adorally.

*Occurrence.*—Upper Cretaceous (Maestrichtian), Escondido formation, Texas.

*Location of type specimen.*—U. S. National Museum.

#### Genus FAURASTER Lambert

*Fauraster* Lambert, in Lambert and Thiéry, 1924. Ess. nom. rais., p. 396. Type species by original designation, *Fauraster priscus* Lambert.

## GENERIC DESCRIPTION

Small, flattened; apical system central, tetrabasal; petals equal, broad, closed, wide interporiferous and poriferous zones; pores conjugate, outer pore slitlike, ambulacral plates single pored beyond petals; periproct supramarginal, very broad, with groove extending to posterior margin; peristome anterior; bourrelets strongly developed, pointed, toothlike; phyllodes unknown but probably single pored.

*Comparison with other genera.*—*Fauraster* is similar to *Faujasia* in having short, closed, equal, petals, a flat adoral surface, and toothlike bourrelets, but is easily distinguished from it by its supramarginal rather than inframarginal periproct, and by its more flattened test. *Fauraster* and *Hardouinia* have similar petals, a supramarginal periproct, and toothlike bourrelets, but the test in *Hardouinia* is much more elevated.

*Range.*—Upper Cretaceous (Maestrichtian) of Spain—only one species known.

## DESCRIPTION OF TYPE SPECIES

## FAURASTER PRISCUS Lambert

Plate 18, figures 6-8

*Fauraster priscus* Lambert, in Lambert and Thiéry, 1924. Ess. nom. rais., pp. 396-397. Described and figured in Lambert, 1927, pp. 39, 40, pl. 3, figs. 1-4.

*Material.*—One specimen, the holotype, was studied. This specimen is very poorly preserved, being fractured and partly covered with matrix, and is evidently the only specimen known of this species.

*Shape.*—Small, holotype 23 mm. long, test greatly flattened with sharp margins; marginal outline angularly circular with width approximately equal to length; adoral surface flat.

*Apical system.*—Central, tetrabasal.

*Ambulacra.*—Petals equal length, short, extending slightly more than half distance to margin, closed, broad with broad tapering interporiferous zones, and broad poriferous zones nearly as wide as interporiferous zones; conjugate with outer pore slitlike, inner pore elongated transversely.

*Periproct.*—Supramarginal, very wide and low, dorsally overhung by upper surface, with flat, broad groove extending from ventral edge of opening to posterior margin.

*Peristome.*—Anterior, small, no other details visible.



*Floscelle*.—Bourrelets strongly developed, toothlike, extending into peristome; phyllodes deeply depressed between bourrelets, broad, no other details visible but probably single pored and similar to those found in *Faujasia* or *Hardouinia*.

*Occurrence*.—Upper Cretaceous (Maestrichtian) at Orrit, Catalonia, Spain.

*Location of type specimen*.—Lambert Collection, Sorbonne, Paris.

*Remarks*.—The holotype is not as well preserved as would appear from a study of Lambert's figures of it. The adoral surface is almost completely covered with matrix, with only a tip of several bourrelets visible. Lambert's figure of the floscelle is largely a reconstruction, and his representation of the structure of the phyllodes may not be correct. The apical system had never been described, although Mortensen (1948, p. 126) suggested that it was probably monobasal, but it is visible on the holotype and is definitely tetrabasal.

#### Genus HARDOUINIA Haime

*Hardouinia* Haime, in D'Archiac and Haime, 1853. Descr. animaux foss. Inde, p. 214. Type species by monotypy, *Pygorhynchus mortonis* Michelin.

Synonyms: *Clarkiella* Lambert; *Cossmannaster* Lambert; *Gonioclypeus* Emmons.

#### GENERIC DESCRIPTION

Medium to large, elongate to circular, often highly inflated, flat adorally, apical system tetrabasal; petals very broad, closed, usually of equal length, pores strongly conjugate, ambulacral plates beyond petals single pored; periproct supramarginal, longitudinal, in groove; peristome central to slightly anterior, pentagonal to circular; bourrelets strongly developed, usually projecting into peristome, often toothlike; phyllodes moderately wide to very wide, single pored, pores in one or two series in each half-ambulacrum, often arranged in arc, widely separated from edge of peristome, deeply depressed between bourrelets; buccal pores present; adorally tubercles much larger than adapically, naked granular zone in middle of interambulacrum 5 and ambulacrum II.

*Comparison with other genera*.—*Hardouinia* appears to be descended from *Petalobrissus*. The older species of *Hardouinia* such as *H. stantoni* (Clark) and *H. bassleri* (Twitchell) are quite similar to some of the species of *Petalobrissus*. They have very similar phyllodes, slightly widened with two series of pores in each half-ambulacrum, a supramarginal, longitudinal periproct, and a similarly shaped test. However, the bourrelets in these older species of *Hardouinia*

are more developed, and the peristome is more central. The later species of *Hardouinia* have much wider, shorter phyllodes with even more developed bourrelets and are easily distinguished from *Petalobrissus*.

*Hardouinia* is similar to *Stigmatopygus* in the shape of its test, position of periproct, prominent bourrelets, and phyllodes, but differs from it by the absence of a deep transverse groove ventral to the periproct, a central peristome, and generally broader petals.

Lambert and Thiéry (1921, p. 361) consider *Hardouinia* a subgenus of *Procassidulus* (herein considered a synonym of *Rhynchopygus*). This genus, however, is quite distinct from *Rhynchopygus*, having a much larger, more inflated test, and much broader petals. Lambert and Thiéry give the age of all the American species they refer to this genus as Eocene or Oligocene, but they are all Upper Cretaceous.

Cooke (1953, p. 19) considered *Australanthus* a synonym of *Hardouinia*, but in *Australanthus* the petals are more open and generally narrower, the apical system is monobasal, and the phyllodes are narrower with far fewer pores.

*Evolution.*—The species of this genus range from the Turonian to the Maestrichtian, with a conspicuous evolutionary trend in the structure of the phyllodes and the bourrelets. The phyllodes become broader, shorter, with fewer pores in the inner series. This reduction of pores in the inner series is away from the peristome with the first pore in the inner series progressively becoming more widely separated from the peristome. In order to avoid subjective selection of species which would favor confirmation of this trend, I have studied the phyllodes of all the known species of *Hardouinia*, in which this area is preserved. They are all figured on chart 7. The age determinations on the species were made by Dr. Norman F. Sohl of the U. S. Geological Survey, who has made detailed studies in the stratigraphy of the Upper Cretaceous in the region where these species occur.

In the earliest known species, *H. stantoni* (Clark) from the Turonian, the phyllodes (chart 7, fig. a) are slightly widened, long, with two series of pores in each half-ambulacrum, with numerous pores in the inner series. In the Santonian species, *H. bassleri* (Twitchell) (chart 7, fig. b), the phyllodes are considerably wider and shorter with approximately the same number of pores in the inner series as in *H. stantoni*. In *H. clypeus* Cooke, also of Santonian age, the phyllodes (chart 7, fig. c) are of similar width and length as *H. bassleri*, but there are more pores in the outer series and they are irregularly arranged. In *H. potosiensis* Lambert, from the Campanian, the phyl-

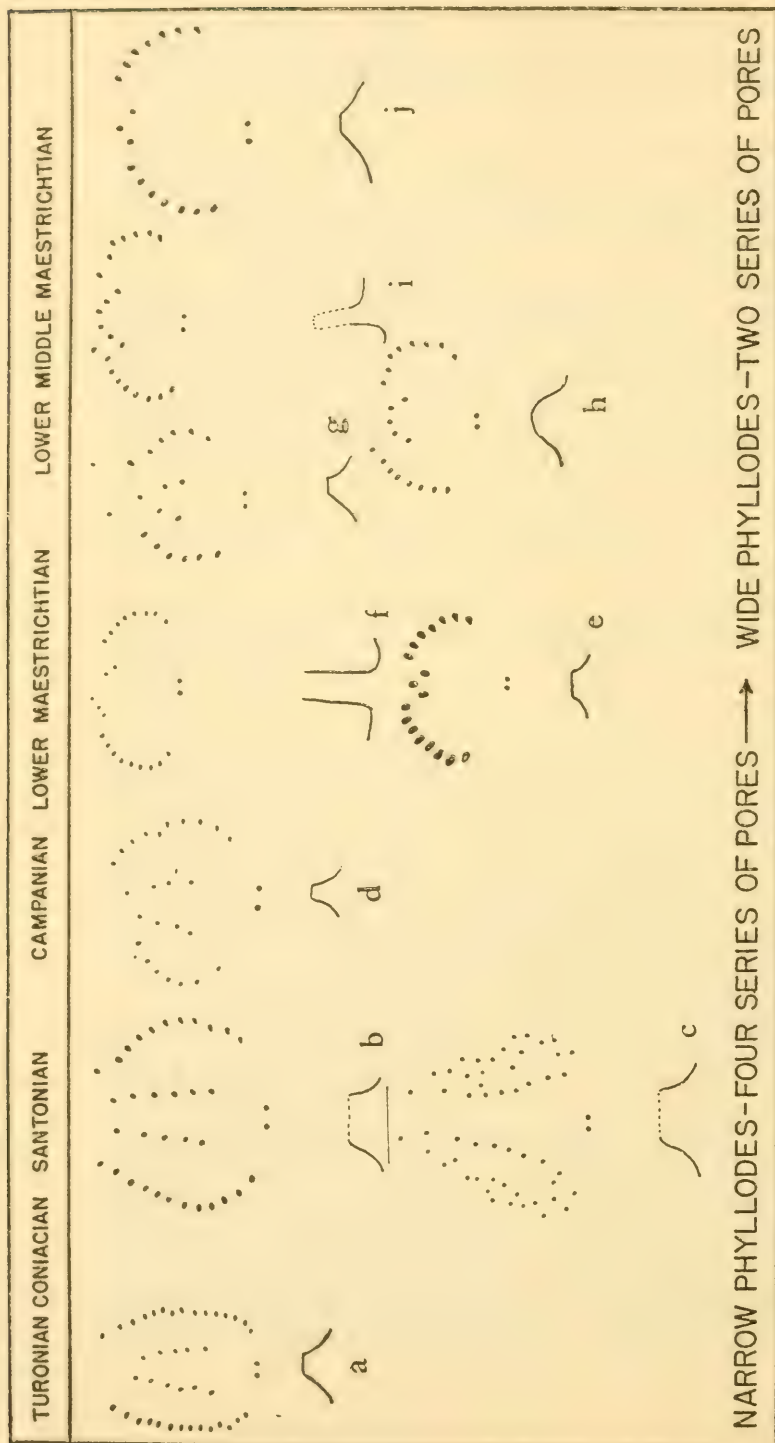


CHART 7.—Phyllodes of species of *Hardouinia* showing an evolutionary trend toward broader, shorter phyllodes with fewer inner pores. a, *Hardouinia stantoni* (Clark); Phyllode of ambulacrum V of holotype, USNM 26268, from the Turonian, Colwell sandstone, 1 mile east of Quillian's ranch on Williams Creek, Huerfano County, Colo.; b, *Hardouinia basifleri* (Whitell); Phyllode of ambulacrum V of USNM 108382, from the Santonian, Tombigbee sand member of the Eutaw formation at Catoma Creek, Montgomery County, Ala.; c, *Hardouinia clypeus* Cooke; Phyllode of ambulacrum V of USNM 17010, from same locality as *H. basifleri* above; d, *Hardouinia pototensis* Lambert; Phyllode of ambulacrum V of USNM 131281a, from the Campanian at San Luis Potosi, Mexico; e, *Hardouinia mortoni* (Michelin); Phyllode of ambulacrum V of USNM 131281b, from the Lower Maestrichtian (Ripley formation) at bluff on right bank of Chattahoochee River near old Alexander Landing, NW 1/4 sec. 9, T. 9 N., R. 20 E., Barlow County, Ala.; f, *Hardouinia torrefacta* (Clark); Phyllode of ambulacrum 5 of USNM 21899, from same locality as *H. mortoni* above; g, *Hardouinia aquorea* (Morton); Phyllode from ambulacrum V of USNM 108383, from the lower Middle Maestrichtian Prairie Bluff chalk, Prairie Bluff, Alabama River, Wilcox County, Ala.; h, *Hardouinia kelliomi* (Stephenson); Phyllode of ambulacrum V of holotype, USNM 73426, from the upper part of the lower Middle Maestrichtian, the Peedee formation, Rock Point Quarries, 1 mile northeast of Rocky Point station, Parker County, N. J.; i, *Hardouinia megalomeryae* Cooke; Phyllode of ambulacrum V of USNM 108384, from the lower Middle Maestrichtian near Yonahblood, Pike County, Ala.; j, *Hardouinia emmonsii* (Stephenson); Phyllode of ambulacrum V from the lower Middle Maestrichtian, upper part of the Peedee formation, Rock Point Quarries; k, middle northeast of Rocky Point station, Parker County, N. J.; l, *Hardouinia* sp. from the lower Middle Maestrichtian, upper part of the Peedee formation, Rock Point Quarries.

lodes (chart 7, fig. d) are even wider, and shorter, with fewer pores in the inner series; and the first pore of the inner series is more distant from the peristome than in the earlier *H. bassleri*. In the Lower Maestrichtian species, *H. mertonis* (Michelin) and *H. porrectus* (Clark), the phyllodes (chart 7, figs. e, f) are much shorter and wider and the inner series more reduced with only one to three pores in each series. In the lower-middle Maestrichtian species *H. meglameryae* Cooke, *H. kellumi* (Stephenson) and *H. aequorea* (Morton), the phyllodes (chart 7, figs. g-i) are similar, but in the latest known species, *H. emmonsii* (Stephenson), the inner series (chart 7, fig. j) is practically absent and the phyllodal pores are arranged in an arc.

There appears to be an evolutionary trend in the structure of the apical system. In the Santonian species *H. bassleri* (text fig. 119) the madreporite is much smaller and the other genital plates larger than in the later species such as *H. potosiensis* (text fig. 120), *H. mertonis* (text fig. 121), *H. porrectus* (text fig. 122), and *H. kellumi* (text fig. 123). Unfortunately, the apical system is not visible in the oldest species, the Turonian *H. stantoni*. It is probable that there is a trend with an increase in the size of the madreporite and a decrease in the other genital plates, but the apical system must be seen on all the species in order to confirm this trend.

*Remarks.*—Weishord's *Clypeopygus habanensis* is herein referred to *Hardouinia* (see p. 70 for discussion).

*Range and distribution.*—Upper Cretaceous (Turonian to Maestrichtian) of the United States, Mexico, and Cuba.

#### DESCRIPTION OF TYPE SPECIES

##### **HARDOUINIA MORTONIS (Michelin)**

Plate 21, figures 1-4; text figures 121, 124; chart 7, figure e

*Pygorhynchus mertonis* Michelin, 1850. Rev. Mag. Zool., ser. 2, vol. 2, p. 240.

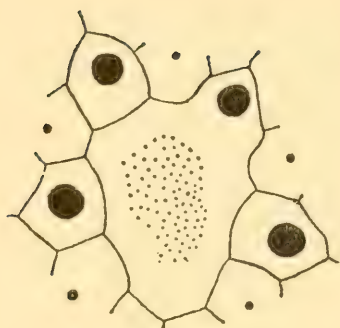
*Material.*—Seventy-five specimens studied in the U. S. National Museum.

*Shape.*—Medium to large, average specimen 50 to 55 mm. long; circular in outline except for pointed posterior; highly inflated; adorally depressed or flat.

*Apical system.*—Slightly anterior, tetrabasal, (text fig. 121) sutures difficult to see; madreporite very large, posteriorly extending between ocular plates V and I, other genital plates very small.

*Ambulacra.*—Petals very well developed, broad, equal length, clos-

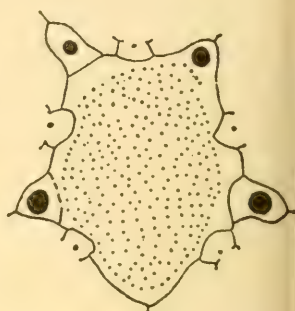




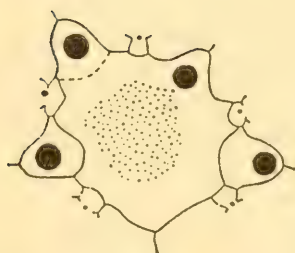
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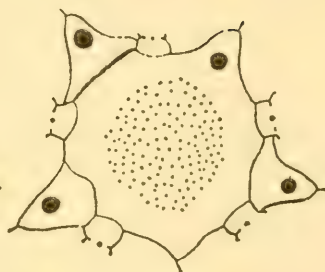
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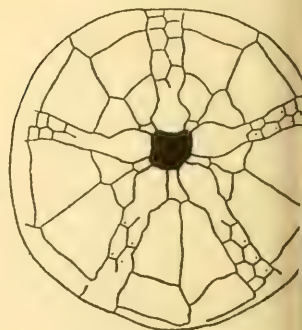
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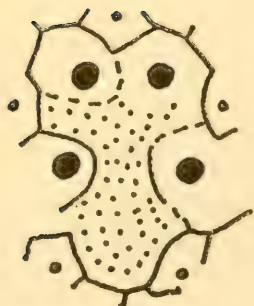
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123



124



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(See legend on opposite page.)

ing distally; interporiferous zones three to four times width poriferous zones; pores conjugate, connected by deep groove, outer pore slitlike, inner pore slightly elongated transversely.

*Adoral interambulacra*.—Single plate at peristome, preceded by two series of alternating plates (text fig. 124), second plate in this series greatly enlarged.

*Periproct*.—Supramarginal, slightly elongated longitudinally, groove originating at periproct continuing to posterior margin of test.

*Peristome*.—Central to slightly anterior, circular opening.

*Floscelle*.—Bourrelets (pl. 21, fig. 4) very strongly developed, toothlike; phyllodes broad, single pored, with pores arranged in arc, ambulacrum deeply depressed near peristome; phyllode of ambulacrum III shorter than others; approximately 18 pores in phyllode III, 22 in phyllodes II and IV, 16 in phyllodes V and I (chart 7, fig. c).

*Tuberculation*.—Adorally tubercles much larger than adapically; naked granular zone in interambulacrum 5.

*Occurrence*.—Upper Cretaceous (Middle Maestrichtian) of southeastern United States.

*Location of type specimen*.—Verneuil Collection, which according to Sherborn (1940, p. 137) is in the École des Mines, Paris.

#### Synonyms of *HARDOUNIA*

*Gonioclypeus* Emmons, 1858. North Carolina Geol. Surv. Rep., Agriculture of the eastern countries, p. 309. Type species by monotypy, *Gonioclypeus subangulatus* Emmons 1838=*Hardouinia mortonis* (Michelin).

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FIGS. 119-127.—119, *Hardouinia bassleri* (Twitchell): Apical system of USNM 108382, from the Santonian, Tombigbee sand member of the Eutaw formation at Catoma Creek, Montgomery County, Ala.,  $\times 21$ . 120, *Hardouinia potosiensis* Lambert: Apical system of USNM 131281, from the Campanian at St. Luis Potosí, Mexico,  $\times 6$ . 121, *Hardouinia mortonis* (Michelin): Apical system of USNM 131257, from lower Maestrichtian, 2.1 miles south of Pontotoc Courthouse, Miss.,  $\times 6$ . 122, *Hardouinia porrectus* (Clark): Apical system of USNM 21890, from lower Maestrichtian (Ripley formation) at bluff on right bank of Chattahoochee River near old Alexander Landing, NW $\frac{1}{4}$  sec. 9, T. 9 N., R. 29 E., Barbour County, Ala.,  $\times 6$ . 123, *Hardouinia kellumi* (Stephenson): Apical system of USNM 73421, paratype, from the lower Middle Maestrichtian from the upper part of the Peedee formation, Rock Point Quarries, 1 mile northeast of Rocky Point station, Pender County, N. C.,  $\times 6$ . 124, *Hardouinia mortonis* (Michelin): Adoral plate arrangement of USNM 131282, from the lower Maestrichtian, Ripley formation, from bluffs of Chattahoochee River 10 miles south of Eufaula, Ala.,  $\times 1$ . 125, 126, *Archiacia palmata* Gauthier: 125, Apical system of holotype in Muséum National d'Histoire Naturelle, Paris, from the Cretaceous (Cenomanian) at Djebel Taferma, Tunisia; 126, Phyllode of ambulacrum IV of specimen in Lambert Collection, Sorbonne, Paris, from the Cretaceous (Cenomanian), Djebel Oum-Ali, Tunisia,  $\times 15$ . 127, *Archiacia saadensis* Peron and Gauthier: Phyllode of ambulacrum II of specimen in Lambert Collection, Sorbonne, Paris, from the Cretaceous (Cenomanian) at Bou Saade, Tunisia,  $\times 8$ .

*Clarkiella* Lambert, 1916a. Rev. crit. palaeozoologie, vol. 20, p. 169. Type species by subsequent designation Lambert and Thiéry (1921, p. 369), *Cassidulus conoideus* Clark (in Clark and Twitchell, 1915) = *Cassidulus hemisphericus* Slocum, 1909, Lambert (1920b, p. 138) proposed a substitute name, *Cossmannaster*, for *Clarkiella*, thinking the latter to be a junior homonym of *Clarkella* Walcott, 1908, a brachiopod. The two names, however, are not spelled the same, and *Clarkiella* is not a junior homonym.

#### DESCRIPTION OF TYPE SPECIES

##### **HARDOUINIA HEMISPHERICA (Slocum)**

Plate 21, figures 6-10

*Cassidulus hemisphericus* Slocum, 1909. Field Mus. Nat. Hist., Geol. ser., vol. 4, No. 1, p. 7, pl. 1, figs. 7-9.

*Material*.—Holotype and a figured specimen studied.

*Shape*.—Medium size, circular in marginal outline, highly inflated, almost as high as long; sides vertical, adoral surface flat; sutures depressed.

*Apical system*.—Anterior, tetrabasal.

*Ambulacra*.—Petals well developed, broad, closing distally, of equal length, extending almost to margin; interporiferous zones wide, twice width of poriferous zones; poriferous zones broad, slightly depressed, pores conjugate, outer pore elongated transversely, slitlike; inner round.

*Periproct*.—Marginal, low on vertical posterior margin, small, longitudinally elongated.

*Peristome*.—Anterior, shape not known.

*Roscelle*.—Bourrelets strongly developed, probably pointed and toothlike; phyllodes single pored, broad, pores arranged in two series in each half-ambulacrum; approximately eight pores in each outer series, two in each inner series; buccal pores present.

*Occurrence*.—Upper Cretaceous (Late Maestrichtian) of southeastern United States.

*Location of type specimen*.—Chicago Museum of Natural History, P. 10347.

*Remarks*.—All authors have considered *Clarkiella* as a separate genus, although Cooke (1953, p. 18) suggested that it might prove to be either a synonym or subgenus of *Hardouinia*. Mortensen separated it because of what he considered to be its distinctive apical system. However, its apical system is very similar to that found in the type species of *Hardouinia*, *H. mortonis*, and it has no genital 5 as suggested by Mortensen.

Genus **AUSTRALANTHUS** Bittner

*Australanthus* Bittner, 1892. Sitzungsab. Kais. Akad. Wiss., vol. 101, p. 350.  
Type species by original designation, *Cassidulus longianus* Gregory.

Medium size, oval, moderately inflated; apical system monobasal; petals short, broad, open, strongly conjugate, with equal poriferous zones, ambulacral plates beyond petals single pored; periproct supra-marginal, longitudinal, narrow; peristome pentagonal; bourrelets very prominent, sharply inflated; phyllodes single pored with few pores; buccal pores present; adorally tubercles much larger, except for wide naked zone in interambulacrum 5.

*Comparison with other genera.*—*Australanthus* is similar to *Hardouinia* in having an inflated test, a supramarginal periproct, prominent, pointed bourrelets, and phyllodes with few pores. It differs in having a monobasal apical system.

Mortensen (1948, p. 222) considered *Australanthus* congeneric with *Procassidulus* and maintained *Procassidulus* even though it is junior. Mortensen was not aware that *Rhynchopygus lapiscancris*, the type species of *Procassidulus* has a tetrabasal apical system which immediately distinguishes it from *A. longianus*. Furthermore, its test is much smaller, and its petals and bourrelets much less developed.

Lambert and Thiéry (1921, p. 363) refer four other species to *Australanthus*, all from the Senonian. One of them, Gabb's *Cassidulus micrococcus*, is a *Hardouinia*. I have not seen any specimens of the other three species, but according to Stoliczka's (1873, pp. 31, 32) descriptions of his *Cassidulus crassus* and *C. emys* their apical systems are tetrabasal, and therefore these two species should not be referred to *Australanthus*. The fourth species, Cotteau's *Cassidulus munieri*, is supposed to be Senonian according to Lambert and Thiéry, although Cotteau (1887, p. 515) says it is from the Lower Eocene. It resembles *Australanthus*, but without seeing specimens of it and without knowing the structure of its phyllodes, I hesitate to refer it to this genus.

*Range and distribution.*—Upper Eocene of Australia.

## DESCRIPTION OF TYPE SPECIES

**AUSTRALANTHUS LONGIANUS** (Gregory)

Plate 27, figures 1-4

*Cassidulus longianus* Gregory, 1890. Geol. Mag., n.s., dec. 3, vol. 7, No. 11, p. 482, pl. 13, figs. 1-3.

*Material.*—Four specimens studied in the British Museum (Natural History), two in the Lambert Collection, Sorbonne, Paris, and eight in the U. S. National Museum.



*Shape*.—Medium size, up to 50 mm. long, oval with smoothly rounded marginal outline, steep sides, slightly flattened adapical surface, with greatest width and height posterior to center.

*Apical system*.—Anterior, monobasal, large central area perforated with madrepore pores, oculars small.

*Ambulacra*.—Petals open, short, extending between one-half and two-thirds distance to margin; petal III longer than paired petals; interporiferous zones slightly narrower than poriferous zones; pores strongly conjugate, outer pore very elongate transversely, inner pore slightly elongated. All petals flush with test. Suture between ambulacra plates passing through pores. Poriferous zones of same petal of equal length.

*Adoral interambulacra*.—Single large plate in each interambulacrum at peristome, preceded by pairs of slightly alternating plates of nearly equal size.

*Periproct*.—Supramarginal, midway between apical system and margin, opening very narrow, longitudinal, in a long narrow groove extending to posterior margin.

*Peristome*.—Anterior, pentagonal, width equaling height.

*Floscelle*.—Bourrelets very prominent, sharply inflated, toothlike. Phyllodes depressed, widened, single pored, very few pores, four in each outer series, only one occluded pore in each phyllode, occurring in right half-area in ambulacrum III, anterior in ambulacrum II and IV, and posterior in I and V; buccal pores present.

*Tuberculation*.—Tubercles much larger adorally, with bosses eccentric anteriorly in large, deep scrobicules; naked area in interambulacrum 5, ambulacrum III.

*Occurrence*.—Upper Eocene of Australia.

*Location of type specimen*.—British Museum (Natural History).

#### Family ARCHIACIDAE Cotteau and Triger, 1869

Medium size, elongate, highly inflated; apical system tetrabasal, very anterior, four genital pores; periproct inframarginal, longitudinal; peristome very eccentric anteriorly, longitudinal; petals broad, closing distally, petal III absent or very short, with doubling of pores; single or double pores in ambulacral plates beyond petals; bourrelets moderately developed; phyllodes slightly widened, double or single pored, two series of pores in each half-ambulacrum, with or without buccal pores; tubercles slightly larger adorally, narrow, naked zone in interambulacrum 5.

*Genera.*—*Archiacia*, *Gentilia*.

*Range.*—Cretaceous (Urgonian-Cenomanian).

*Comparison with other families.*—The Archiacidae are distinguished by the absence or great reduction of a petal in ambulacrum III, and the doubling of pores in ambulacrum III.

**Genus ARCHIACIA L. Agassiz**

*Archiacia* L. Agassiz, in Agassiz and Desor, 1847. Ann. Sci. Nat., ser. 3, vol. 7, p. 159. Type species, *Archiacia sandalina* Agassiz, by subsequent designation. d'Orbigny (1856, p. 284).

GENERIC DESCRIPTION

Medium size, elongate, adapically high, in some species very inflated anteriorly, oral surface flat or sunken around peristome; apical system very eccentric anteriorly, tetrabasal, madreporite extending posterior to posterior genital plates; petals short or long, anterior petals (II and IV) curving posteriorly, shorter than posterior petals, pores conjugate, in some species outer pore very elongated obliquely; ambulacrum III not petaloid, often in a groove, usually with double series of pore pairs in each half-ambulacrum; periproct inframarginal, longitudinal; peristome central or anterior, longitudinal or transverse; bourrelets present, phyllodes broad, double pored, with approximately six pore pairs in each outer series and three or four in each inner.

*Comparison with other genera.*—*Archiacia* is most similar to *Gentilia*, both genera having inflated tests, nondeveloped or short petals III with doubling of the pores in the ambulacral plates beyond the petal. *Archiacia* differs in having double pores in its ambulacral plates beyond the petals and is probably ancestral to *Gentilia*.

*Remarks.*—The apical system has not been figured in most of the species of this genus. Mortensen (1948, p. 319) suggested, after noting Gauthier's (1889a, pl. 2, fig. 7) inaccurate figure of the apical system in *Archiacia palmata* Gauthier, that the apical system in *Archiacia* was typically monobasal. I have studied both the holotype of *A. palmata* in the d'Orbigny Collection in the Muséum National d'Histoire Naturelle and three specimens in the Lambert Collection at the Sorbonne, Paris. The apical system (text fig. 125) is definitely tetrabasal with genital 2 extending posteriorly. The genital plates are not arranged in a cruciform fashion as shown in Gauthier's figure. I also saw the apical system in *Archiacia santonensis* d'Orbigny on a specimen in the d'Orbigny Collection, and it is very similar,

being tetrabasal with genital 2 also extending posteriorly. Szörényi (1955b, text fig. 5) shows a monobasal apical system in her *Archiacia hungarica*, but I suspect that her figure is inaccurate. The shape of the genital plates and the location of the madreporic pores suggests a tetrabasal system.

The floscelle is very similar in most of the species of *Archiacia*. As the phyllodes have not been figured before in this genus, I include a drawing of a phyllode of *A. palmata* (text fig. 126) and *A. saadensis* Peron and Gauthier (text fig. 127), and photographs (pl. 22, figs. 7-9) of *A. palmata*.

Szörényi (1955a, text fig. 6) shows single pores in ambulacrum III of *Archiacia hungarica*. As all the specimens of *Archiacia* that I have seen have the pores paired, I suspect that her drawing is incorrect and that they are pore pairs.

*Ecology*.—Szörényi (1955b, pp. 383-384) suggested that the high test of echinoids of this genus, with the petals near the apex, indicate that they lived partially buried on the sea floor.

*Range and distribution*.—Cretaceous (Cenomanian) of the circum-Mediterranean countries; Szörényi (1955a) has described two species from the Lower Cretaceous (Urgonian to Aptian) of Bakony.

#### DESCRIPTION OF TYPE SPECIES

#### ARCHIACIA SANDALINA L. Agassiz

Plate 22, figures 4-6

*Archiacia sandalina* L. Agassiz, in Agassiz and Desor, 1847. Ann. Sci. Nat., ser. 3, vol. 7, p. 159; figured in Ann. Sci. Nat., ser. 3, vol. 6 (1846), pl. 15, figs. 24-26, not figs. 27, 28 as stated by Agassiz. Although this species was figured by Agassiz in 1846, there was no plate explanation and the species must date from his description. Many authors have attributed this species to d'Archiac. However, the manuscript in which he referred to this name was never published.

*Material*.—I studied one specimen in the d'Orbigny Collection in the Museum National d'Histoire Naturelle. This is evidently the specimen referred to by d'Orbigny (1856, p. 285) but not the specimen he figured. The specimen is fairly well preserved, although part of the apical system and peristome is absent.

*Shape*.—Medium size (approximately 30 mm. in length), elongate, with adapical surface strongly inflated anteriorly, with pointed prominence overhanging anterior margin; adorally margin flat, but depressed around peristome.

*Apical system*.—Small, very eccentric anteriorly, tetrabasal, but owing to poor preservation, no other details visible.

*Ambulacra*.—Petals short, narrow, with slight tendency to close distally; interporiferous zones almost twice width of poriferous zones; pores conjugate, outer pore slightly elongate transversely. Petals II and IV transverse or curving posteriorly. Ambulacrum III not petaloid, arrangement of pore pairs not clear on specimen studied.

*Periproct*.—Inframarginal, longitudinal.

*Peristome*.—Slightly anterior, partially destroyed in specimen studied, but from d'Orbigny's figure (1856, pl. 909, fig. 8), slightly longitudinal.

*Floscelle*.—Bourrelets present; phyllodes broad (text fig. 127 for *A. saadensis*), double pored with approximately six pore pairs in each outer series and three or four in the inner series in each half-ambulacrum; no buccal pores.

*Occurrence*.—Cretaceous (Cenomanian) at Fourras, Charras, and Port-des-Barques (Charente-Inferieure), France; Djebel Maghila, Fom-el-Guelta; Djebel Cehela, Tunisia; Ain Baira and Bou-Saada, Algeria.

*Location of type specimen*.—Holotype apparently lost, but plaster cast in Museum d'Histoire Naturelle, Neuchâtel, Switzerland (Lambert and Jeannet, 1928, p. 198).

#### Genus GENTILIA Lambert

*Gentilia* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 55, p. 35. Type species *Gentilia tafleltensis* Lambert by subsequent designation Lambert (1920a, p. 154).

Synonym: *Thomasaster* Lambert.

#### GENERIC DESCRIPTION

Medium size, usually inflated, greatest width posterior, slightly pointed posterior margin, steep sides, flat adoral surface; apical system anterior, tetrabasal; petals very broad, closed distally, unequal, petal III absent or very short, interporiferous zones very broad, poriferous zones narrow, pores conjugate, outer pore slitlike; periproct inframarginal, large, slightly longitudinal; peristome longitudinal, flush with test; bourrelets slightly developed; phyllodes widened, single pored with two series of pores in each half-ambulacrum; buccal pores absent or slightly developed; adorally tubercles approximately same size as adapically, very narrow naked granular zone in interambulacrum 5.



*Comparison with other genera.*—*Gentilia* is most similar to *Archiacia*, for in both genera ambulacrum III is absent or slightly developed, the periproct is inframarginal, the test well inflated, the petals broad, the peristome longitudinal, and the phyllodes have two series of pores in each half-ambulacrum. *Gentilia* differs in having single pores in its ambulacral plates beyond the petals and in the phyllodes, whereas in *Archiacia* they are double pored, and in *Gentilia* the apical system is less anterior.

*Remarks.*—I was unable to find any specimens of the type species in Paris but did study a specimen from the Lambert Collection labeled ? *Gentilia globosa* Lambert. I have not been able to find any description of this species in the literature, and it is so similar to the type species, *Gentilia tafileltensis*, that it may be conspecific. I include photographs (pl. 23, figs. 3, 4) of this specimen and a drawing of one its phyllodes (text fig. 128). In the collections at the Muséum National d'Histoire Naturelle in Paris I found several specimens labeled *Pyguropsis noetlingi* which belong to a new species of *Gentilia*, described below.

In the specimen labeled ? *Gentilia globosus* and here provisionally referred to *G. tafileltensis* there are no buccal pores. This is the only specimen I have ever seen of a cassiduloid that had single-pored phyllodes but no buccal pores. This specimen is Cenomanian, and that is the time when the buccal pores and single-pored phyllodes first appeared. In the new species of *Gentilia*, *G. syriensis*, there are buccal pores but they are very minute. Again this species is Cenomanian.

*Range and distribution.*—Cretaceous (Cenomanian) of Egypt, Syria, and Morocco.

#### DESCRIPTION OF NEW SPECIES

##### GENTILIA SYRIENSIS Kier, new species

Plate 23, figures 5-11; text figures 129-131

*Material.*—Eight specimens studied in the Muséum National d'Histoire Naturelle in Paris.

*Shape.*—Medium size, holotype 33 mm. long, broad with greatest width posterior to center, rounded anterior margin, slightly pointed posterior; steep sides, flat adoral surface.

*Apical system.*—Anterior, tetrabasal, four genital pores.

*Ambulacra.*—Petals very broad, closing distally, with very broad interporiferous zones, narrow poriferous zones with strongly con-

jugate pores, outer pore slitlike; petals V and I longer than others, petal III very short, widely open; beyond petaloid portion single pore in each ambulacral plate but with pores arranged in double series (text fig. 131) almost to margin; ambulacral plates beyond other petals single pored.

*Periproct*.—Inframarginal, slightly longitudinal, opening very large.

*Peristome*.—Very eccentric anteriorly, higher than wide, pentagonal.

*Floscelle*.—Bourrelets slightly developed; phyllodes (text fig. 129) slightly widened, single pored, pores in two series in each half-ambulacrum, five to six pores in each series; minute buccal pores (text fig. 130).

*Tuberculation*.—Adorally, tubercles only slightly larger than adapically, narrow naked granular zone in interambulacrum 5.

*Occurrence*.—Cretaceous (Cenomanian) of Syria; collected by Dubertret.

*Location of type specimen*.—Holotype in Muséum National d'Histoire Naturelle, Paris.

#### Synonym of GENTILIA

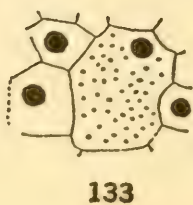
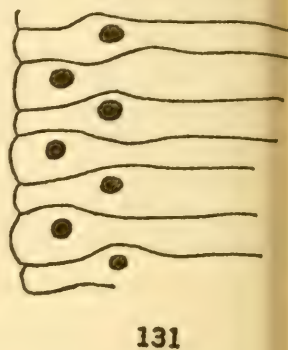
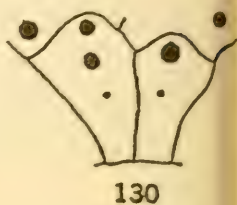
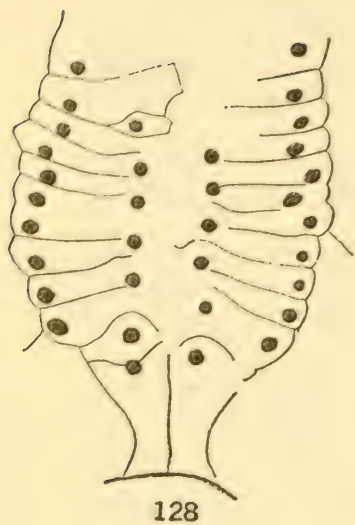
*Thomasaster* Lambert, 1920b. Rev. crit. paléozool., vol. 24, p. 138; pro *Thomasia* Lambert, 1918; non Poche, 1900; nec. Ruebsaamen, 1910. Type species by original designation, *Archiacia araidahensis* Gauthier.

*Remarks*.—Both Lambert (1937, p. 78) and Mortensen (1948, p. 325) suggested that *Thomasaster* probably was not distinct from *Gentilia*. I have not seen any specimens of the type species, but from Gauthier's description, it appears to be congeneric with *Gentilia*.

#### Family CASSIDULIDAE Agassiz and Desor, 1847

Small to large, elongate, flat adoral surface; apical system anterior, tetrabasal or monobasal; periproct supramarginal to marginal, longitudinal or transverse; peristome anterior, oval or pentagonal, transverse; petals broad, usually equal length, often inconspicuous, poriferous zones of unequal length in most Tertiary species, ambulacral plates beyond petals double pored in pre-Senonian species; bourrelets well developed; phyllodes widened, double or single pored, one or more series of pores in each half-ambulacrum; buccal pores absent in pre-Senonian species; tubercles much larger adorally than adapically, naked granular zone in interambulacrum 5.

*Genera*.—*Rhynchopygus*, *Nucleopygus*, *Hypsopygaster*, *Ochetes*, *Cassidulus*, *Rhyncholampas*.



(See legend on opposite page.)

*Range*.—Lower Cretaceous (Albian) to Recent.

*Comparison with other genera*.—The Cassidulidae are most similar to the Nucleolitidae, from which they differ in having more developed bourrelets, wider phyllodes with fewer pores, a naked, often pitted zone adorally in interambulacrum 5, and larger tubercles adorally.

#### Genus RHYNCHOPYGUS d'Orbigny

*Rhynchopygus* d'Orbigny, 1850. Pal. franc., Crétacé, vol. 6, p. 323. Type species by virtual monotypy, *Cassidulus marmini* Agassiz. d'Orbigny referred another species to this genus, but since he questioned whether it really belonged to the genus, it is not available as type species.

Synonyms: ? *Paralamphas* Duncan and Sladen; *Procassidulus* Lambert.

#### GENERIC DESCRIPTION

Small, low, oval, or with greatest width posterior to center, anterior margin smoothly rounded, posterior often pointed, anterior adapical surface gently curved, posterior often truncated obliquely; adoral surface flat; apical system anterior, tetrabasal, four genital pores; petals slightly or well developed, equal or with ambulacrum III longer than others, open or closing distally, conjugate pores, ambulacral plates beyond petals with single pores; periproct supra-marginal, transverse or longitudinal, groove extending from opening to posterior margin; peristome, central to anterior, circular to oval; bourrelets well developed, often pointed; phyllodes widened, single pored, with slight crowding, only few pores occluded; buccal pores present; tubercles adorally much larger; naked, often pitted, median area in interambulacrum 5, ambulacrum III.

*Comparison with other genera*.—*Rhynchopygus* is very similar to *Cassidulus* but differs in having a tetrabasal apical system. It is

Figs. 128-136.—128, *Gentilia tajfeliensis*? Lambert: Phyllode of ambulacrum IV of specimen in the Lambert Collection, Sorbonne, Paris, probably from the Cretaceous (Cenomanian) at Riz el Abiod,  $\times 10$ . 129-131, *Gentilia syriensis* Kier: 129, Phyllode of ambulacrum IV of specimen in Muséum National d'Histoire Naturelle, Paris, from Cretaceous (Cenomanian) of Syria,  $\times 10$ ; 130, enlarged view of adoral portion of same phyllode showing minute buccal pores,  $\times 15$ ; 131, view of left poriferous zone of ambulacrum III adoral to petaloid portion showing arrangement of pores into two series, on same specimen as figure 130,  $\times 20$ . 132, 133, *Rhynchopygus lusitanicus* (De Loriol): 132, Phyllode of ambulacrum V of USNM 131264, from the Upper Cretaceous (Lower Turonian) at Pognadoresses (Gard), France,  $\times 20$ ; 133, apical system of same specimen,  $\times 20$ . 134, *Rhynchopygus marmini* (Agassiz): Apical system of USNM 19559, from the Upper Cretaceous (Senonian) at Port Brehay, Manche, France,  $\times 15$ . 135, 136, *Rhynchopygus lapiscaneri* (Leike): 135, Apical system of USNM 131263, from the Upper Cretaceous (Maestrichtian) at St. Pietersberg, Belgium,  $\times 15$ ; 136, phyllode of ambulacrum V of USNM 131260, from the Upper Cretaceous (Maestrichtian) at Beeringen (Charb.), Belgium,  $\times 15$ .



probably the ancestor of *Cassidulus*. It differs from *Nucleopygus* in having much more pronounced bourrelets, more widened phyllodes, larger adoral tubercles, and a wider naked zone in interambulacrum 5.

*Remarks.*—Mortensen was not aware that the apical system in *Rhynchopygus marmini* was tetrabasal and considered *Rhynchopygus* as a synonym of *Cassidulus*. I have also found a tetrabasal apical system in *Rhynchopygus macari* (Smiser) and in *Rhynchopygus lapiscancrini* (Leske). These three species have many features in common and appear to be clearly congeneric, and distinct from *Cassidulus*. They are small forms with supramarginal periprocts (the fact that the periproct is transverse in *R. marmini* and *R. macari* and longitudinal in *R. lapiscancrini* does not seem to be of generic significance), similar petals, and flat adoral surfaces. Their close relationship is shown strikingly by their identical floscelles with extremely well-developed bourrelets and broad, similar phyllodes.

*Rhynchopygus lusitanicus* (De Loriol) from the lowest Turonian is the oldest species of this genus that I have studied. Its apical system (text fig. 133) is tetrabasal not monobasal as previously thought. Its phyllodes (text fig. 132) have more pores than found in the Senonian species of this genus, confirming the suggestion made herein that the number of phyllodal pores is reduced in many genera in time.

Kew (1920, pp. 138-142) placed all the American west coast species of cassidulids in *Rhynchopygus*, which he considered to be a subgenus of *Cassidulus*. I have studied the type specimens of these species and do not believe that any of them belong in *Rhynchopygus*. They all have monobasal apical systems; three of them, *C. ellipticus* Kew, *C. californicus* Anderson, and *C. ynezensis*, are herein referred to *Cassidulus* and *C. mexicanus* Kew to *Rhyncholampas*.

*Range and distribution.*—Upper Cretaceous (Turonian-Maestrichtian) of Belgium, Holland, and France. The distribution of this genus will not be known until all the species previously referred to *Cassidulus* have been reexamined and their apical systems studied.

#### DESCRIPTION OF TYPE SPECIES

##### **RHYNCHOPYGUS MARMINI (L. Agassiz)**

Plate 24, figures 1-4; text figures 134, 137

*Cassidulus marmini* L. Agassiz, in L. Agassiz and Desor, 1847. Ann. Sci. Nat., ser. 3, vol. 7, p. 157.

*Material.*—Twelve specimens studied in the U. S. National Museum, and several in the Lambert Collection at the Sorbonne, Paris.

*Shape*.—Small, usually less than 15 mm. long; anterior, posterior margin smoothly rounded, sides straight, adapically slightly inflated, with posterior surface obliquely truncated; adorally flattened.

*Apical system*.—Slightly anterior, tetrabasal (text fig. 134), four genital pores, madreporite extending posteriorly, separating posterior genital and ocular plates.

*Ambulacra*.—Petals very inconspicuous, difficult to see on well-preserved specimens; narrow with narrow interporiferous zones, petals III longer than others, open, other petals slightly closed; pores conjugate, outer pore slightly elongated transversely.

*Periproct*.—Supramarginal, transverse, small, opening in underside of large overhang, with deep transverse indentation dorsal to it; opening not in this transverse indentation as formerly supposed.

*Peristome*.—Slightly anterior, circular.

*Floscelle*.—Bourrelets strongly developed, pointed, phyllodes (text fig. 137) widened, single pored, broad, with four pores in each outer series, and one to two in each inner; buccal pores present; sphaeridia in two series along midline of each ambulacrum.

*Tuberculation*.—Adapically, tubercles very small, covering whole surface, obscuring petals; adorally tubercles larger, except for naked, pitted medial area in interambulacrum 5, ambulacrum III.

*Occurrence*.—Upper Cretaceous (Maestrichtian), Holland, France.

*Location of type specimen*.—Unknown.

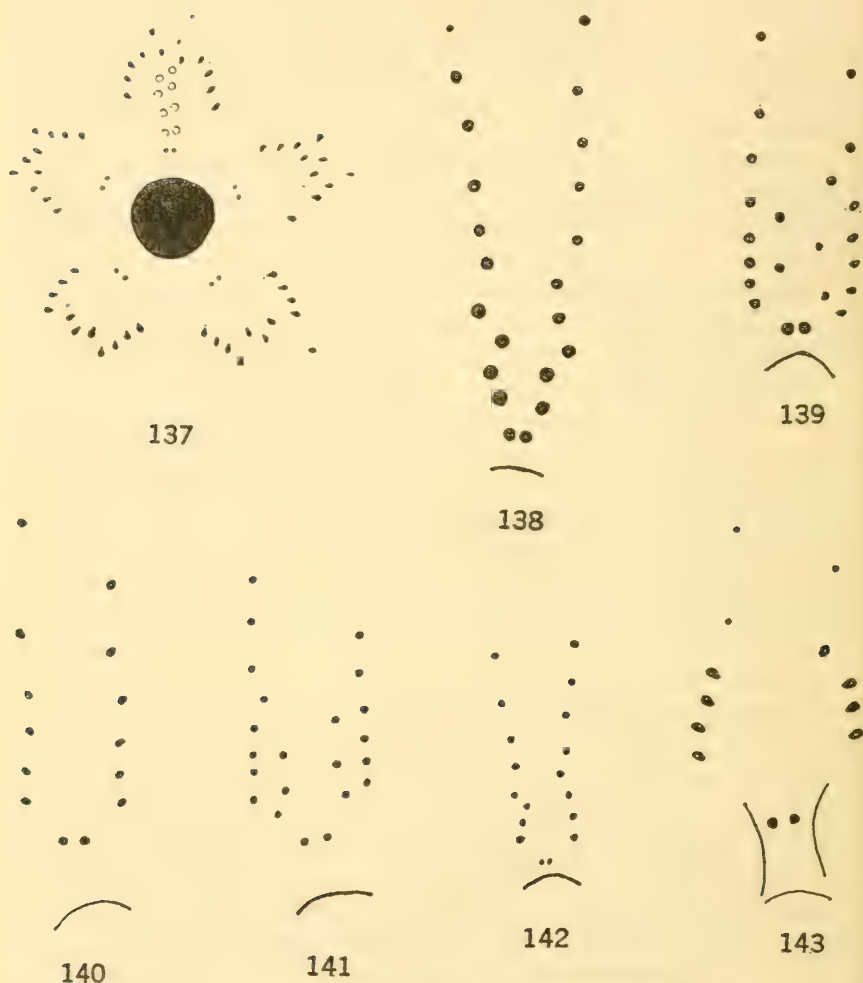
*Remarks*.—d'Orbigny's (1856, pl. 927) figures of this species are erroneous in several important details. He shows a wide bilobed opening for the periproct, whereas in reality the opening is much smaller and occurs on the lower side of the overhang, not in the surface posterior to the overhang as shown in his figure. The bourrelets are pointed, not bulbous, and there are very few pores in the phyllodes, not many as shown in his drawing. d'Orbigny does not show the naked, pitted zone in interambulacrum 5 and ambulacrum III, and the petals are not as conspicuous as he depicts them.

### ? *Synonym of RHYNCHOPYGUS*

*Paralamphas* Duncan and Sladen, 1882. Pal. Indica, ser. 14, vol. 1, pt. 3, p. 72.

Type species, *Paralamphas pileus* Duncan and Sladen, by subsequent designation, Lambert and Thiéry, 1921, p. 371.

*Remarks*.—This genus was erected by Duncan and Sladen for two species from the Paleocene of India which differ from *Cassidulus* by having a higher test and lacking a naked medial zone in interambulacrum 5 and ambulacrum III. The higher test does not seem to me



FIGS. 137-143.—137, *Rhynchopygus marmini* (Agassiz): Floscelle of specimen in Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Maestrichtian) at Fresville, France,  $\times 6$ . 138, *Nucleopygus minimus* (d'Orbigny): Phyllode of ambulacrum V of specimen in Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Senonian) at St. Paterne, France,  $\times 15$ . 139, *Nucleopygus parallelus* (Agassiz): Phyllode of ambulacrum V of USNM 131283, from the Upper Cretaceous (Turonian) at Bousse, France,  $\times 15$ . 140, *Nucleopygus minor* Desor: Phyllode of ambulacrum V of specimen 2523 in the Museum of Comparative Zoology, Harvard, from the Upper Cretaceous (Senonian) at Royan, France,  $\times 15$ . 141, *Nucleopygus angustatus* (Clark): Phyllode of ambulacrum II of holotype, USNM 103701, from the Cretaceous (Cenomanian), Buda limestone, Shoal Creek, Austin, Tex.,  $\times 15$ . 142, *Nucleopygus scrobiculatus* (Goldfuss): Phyllode III of USNM 131278, from the Upper Cretaceous (Maestrichtian) from top of quarry of Kalkmergelmaatschappij, St. Pietersberg, Belgium,  $\times 15$ . 143, *Hypsopygaster ungosensis* Bajarunas: Phyllode of ambulacrum V, from specimen in Geologic Museum of RAN, Russia, from the Danian, at Ungozya, Mangyshlak, Russia,  $\times 15$ .

to be an important character worthy of generic distinction, but the absence of the naked area is significant. Unfortunately, I have been unable to study any specimens of their two species, and Duncan and Sladen do not figure well the adoral surfaces of either species. Until this area has been reexamined, it seems best to consider this genus tentatively as a synonym of *Rhynchopygus*. Lambert (in Besairie and Lambert, 1930, p. 114) describes another *Paralampas*, *P. besairiei*, but again his figures do not clearly show this median zone. Fischer (1951, pp. 69, 71) refers *Rhyncholampas lyelli* (Conrad) and *Rhyncholampas globosus* (Fischer) to *Paralampas*, and considers *Paralampas* as a subgenus of *Cassidulus*. Both of these species, however, have a naked medial zone adorally, and should be referred to *Rhyncholampas*.

#### Synonym of RHYNCHOPYGUS

*Procassidulus* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 55, p. 33.  
Type species by original designation, *Echinites lapiscanceri* Leske.

#### DESCRIPTION OF TYPE SPECIES

##### RHYNCHOPYGUS LAPISCANCRI (Leske)

Plate 24, figures 5-8; text figures 135, 136

*Echinites lapis-canceri* Leske, 1778. Klein's Naturalis dispositio echinodermatum, p. 256, pl. 43, figs. 10, 11.

*Material*.—Fifty-two specimens studied in the U. S. National Museum.

*Shape*.—Small, elongate, smoothly rounded anterior margin, pointed posterior margin, flattened adoral surface, greatest width posterior to center, greatest height at center, oblique posterior face.

*Apical system*.—Tetrabasal (text fig. 135), anterior, madreporite extending posteriorly separating posterior genital and ocular plates.

*Ambulacra*.—Petals of unequal length, petal III the longest, extending over two-thirds distance to margin, petals II and IV over one-half, petals V and I the shortest, less than one-half; pores conjugate, outer pore slightly elongated transversely; interporiferous zones twice width of poriferous zones at greatest width; petals closing distally.

*Periproct*.—Supramarginal, midway between apical system and posterior margin, oval, slightly elongated longitudinally; slight groove extending posteriorly.

*Peristome*.—Anterior, pentagonal, higher than wide.



*Floscelle*.—Bourrelets strongly developed, highly inflated, pointed; phyllodes single pored (text fig. 136), broad, with five to seven pores in each outer series and one to three in each inner series; buccal pores present.

*Tuberculation*.—Adorally, tubercles much larger, bosses anterior, in deep, anteriorly elongated scrobicules; naked pitted medial area in interambulacrum 5, ambulacrum III.

*Occurrence*.—Maestrichtian of France, Belgium, and Holland.

*Location of type specimen*.—Unknown.

*Remarks*.—Lambert created *Procassidulus* as a substitute name for *Cassidulus* which he thought was preoccupied.

#### Genus NUCLEOPYGUS L. Agassiz

*Nucleopygus* L. Agassiz, 1840a. Catalogus systematicus ectyporum echinodermatum fossilium musei Neocomensis, pp. 7, 17. Type species by subsequent designation, Lambert, 1898, p. 165, *Nucleopygus minor* Desor.  
Synonyms: *Lychnidius* Pomel; *Porobrissus* Lambert.

#### GENERIC DESCRIPTION

Small, low, generally oval, well-rounded margin, depressed peristome; apical system tetrabasal, often very eccentric anteriorly; petals narrow, inconspicuous, usually open, with conjugate pores, ambulacral plates beyond petals single pored; periproct supramarginal, longitudinal, in groove extending to posterior margin; peristome pentagonal or subpentagonal, anterior; bourrelets slightly to moderately developed, not pointed; phyllodes single pored, narrow or only slightly widened, very few or no occluded pores; buccal pores present; adoral tubercles of same size or only slightly larger than adapical, very narrow naked zone often in interambulacrum 5, often pitted.

*Comparison with other genera*.—*Nucleopygus* is similar to *Nucleolites* in having a supramarginal periproct and short petals, but differs in having less conspicuous, narrower petals, a more elongate test, and single-pored phyllodes with buccal pores. It differs from *Petalobrissus* in having narrower petals, a smaller test, and narrower phyllodes with fewer occluded pores. It is similar to *Rhynchopygus* in its petals and shape and size of test, but is distinguished from it by its less developed bourrelets, narrower phyllodes, and smaller adoral tubercles. Finally, it differs from *Ochetes* in having less developed bourrelets, single pored phyllodes, more developed petals, and smaller adoral tubercles.

*Range and distribution.*—Upper Cretaceous (Cenomanian to Maastrichtian) of Europe, Africa, and United States. Lambert and Thiéry give a much wider range to this genus, from the Aptian to Recent. However, the Aptian species, Desor's *Echinobrissus placentula*, is not a *Nucleopygus*. I have seen specimens of this species; its phyllodes are double pored and it should be referred to *Nucleolites*. The oldest specimens I have seen of *Nucleopygus* were from the Cenomanian, Gres Vert, at Le Mans. These specimens, which are in the École National Supérieure des Mines in Paris, were labeled *Nucleolites lacunosus* but resemble more closely d'Orbigny's *Echinobrissus similis*. They have single-pored phyllodes and definitely belong in *Nucleopygus*. A photograph of the adapical surface of one of them is included herein (pl. 24, fig. 9). I have also seen specimens of Agassiz's *Nucleolites parallelus* from the Turonian, and d'Orbigny's *Echinobrissus minimus* from the Senonian. Both of these species have single-pored phyllodes (text figs. 138, 139) with very few pores, small tests, slightly developed petals, and a supra-marginal periproct, all characters typical of *Nucleopygus*. Of the three post-Cretaceous species that Lambert and Thiéry refer to *Nucleopygus*, Edwards' *Nucleolites recens* is the type species of another genus, *Apatopygus*; Cotteau's *Echinobrissus delfortricri* and Zittel's *Nucleolites papillosus* may each be a *Cassidulus*.

#### DESCRIPTION OF TYPE SPECIES

##### NUCLEOPYGUS MINOR Desor

Plate 24, figures 10, 11; text figure 140

*Nucleopygus minor* Desor, 1842. Des galérites, p. 33, pl. 5, figs. 20-22.

*Material.*—Nine specimens studied in the Lambert Collection at the Sorbonne, one in the Muséum National d'Histoire Naturelle, Paris, and three in the Museum of Comparative Zoology, Harvard.

*Shape.*—Very small, usually less than 8 mm. long, moderately inflated with greatest height anterior to center, greatest width posterior; anterior margin smoothly rounded, posterior slightly truncated by anal groove; sides smoothly rounded, adoral surface depressed at peristome.

*Apical system.*—Anteriorly eccentric, tetrabasal, with four genital pores.

*Ambulacra.*—Petals inconspicuous, narrow, open, flush with test, short, petal III shorter than others, inner pore of pore pair round, outer round or slightly elongate transversely, conjugate.

*Periproct*.—Supramarginal, longitudinal, in deep groove extending posteriorly to margin.

*Peristome*.—Anterior, depressed, subpentagonal, wider than high.

*Floscelle*.—Bourrelets moderately developed, vertical sides; phyllodes single pored, not widened, only slight crowding of pores (text fig. 140); buccal pores present.

*Tuberculation*.—Adorally, pores only slightly larger than adapically.

*Occurrence*.—Upper Cretaceous (Senonian), Royan, St. Paterne, France.

*Location of type specimen*.—According to Desor (1858, p. 266) in the Michelin Collection, which according to Lambert and Jeannet (1928) is in the École National Supérieure des Mines in Paris. I was unable to find the specimen there.

*Remarks*.—This species has been attributed by most workers to Agassiz (1840a), but it is a nomen nudum in that reference.

#### Synonym of NUCLEOPYGUS

*Lychnidius* Pomel, 1883. Class méth., p. 55. Type species by monotypy, *Nucleolites scrobiculatus* Goldfuss.

*Remarks*.—*Lychnidius* is indistinguishable from *Nucleopygus*. Its type species is very similar to the type species of *Nucleopygus* and certainly congeneric with it. In both species the test is small, elongate, with supramarginal, longitudinal periproct, inconspicuous petals, pentagonal transverse peristome, moderately developed bourrelets, slightly crowded single-pored phyllodes, and tetrabasal apical system.

#### DESCRIPTION OF TYPE SPECIES

##### NUCLEOPYGUS SCROBICULATUS (Goldfuss)

Plate 25, figures 1-4; text figure 142

*Nucleolites scrobiculatus* Goldfuss, 1826. Petrefacta Germaniae, p. 138, pl. 43, fig. 3.

*Material*.—Sixteen specimens studied in the U. S. National Museum.

*Shape*.—Very small, oval, inflated, rounded margin.

*Apical system*.—Anterior, tetrabasal (for an excellent description and figures, see Engel and Meijer (1957, p. 91, text figs. 1, 2).

*Ambulacra*.—Petals slightly developed, short, with slight tendency to close distally; interporiferous zones approximately same width as

poriferous; pores slightly conjugate, both inner and outer pore of pair round; ambulacral plates single pored beyond petals.

*Periproct*.—Supramarginal, longitudinal, high on slight posterior truncation.

*Peristome*.—Central, depressed, subpentagonal, vertically walled.

*Floscelle*.—Bourrelets vertical, slightly inflated; phyllodes single pored, no widening of area, slight crowding (text fig. 142).

*Tuberculation*.—Adorally, tubercles of approximately same size as adapically; slight naked, granular zone in interambulacrum on some specimens, absent on others.

*Occurrence*.—Upper Cretaceous (Maestrichtian) of Holland and Belgium.

*Location of type specimen*.—University of Bonn, Germany.

#### Synonym of **NUCLEOPYGUS**

*Porobrissus* Lambert, 1916. Rev. crit. palaeozool., vol. 20, p. 169. Type species by monotypy, *Echinobrissus angustatus* Clark, 1915.

#### DESCRIPTION OF TYPE SPECIES

#### **NUCLEOPYGUS ANGUSTATUS (Clark)**

Plate 24, figures 12, 13; text figure 141

*Echinobrissus angustatus* Clark, in Clark and Twitchell, 1915. U. S. Geol. Surv. Monogr. 54, p. 69, pl. 27, figs. 2a-c.

*Material*.—Eighteen specimens studied in the collection of University of Texas, and holotype and paratype in U. S. National Museum.

*Shape*.—Small, average 15 mm. long, oval, low, greatest width posterior to center, greatest height anterior, adoral surface depressed around peristome.

*Apical system*.—Very eccentric anteriorly, tetrabasal, with genital 2 extending posteriorly separating posterior oculars.

*Ambulacra*.—Petals slightly developed, short, petal III shorter than others, closing slightly distally, interporiferous zones equal in width to poriferous zones; outer pore very slightly elongated transversely, inner pore round, conjugate.

*Periproct*.—Supramarginal, midway between apical system and posterior margin; elongate longitudinally, in groove extending to posterior margin.

*Peristome*.—Anterior, oval transversely, depressed.

*Floscelle*.—Bourrelets slightly developed, phyllodes slightly developed (text fig. 141), single pored, six pores in each outer series, three to four in each inner series; buccal pores present.



*Tuberculation*.—Adorally tubercles only slightly larger than adapically.

*Occurrence*.—Upper Cretaceous (Cenomanian), Buda limestone, Shoal Creek, Austin, Tex.

*Location of type specimen*.—U. S. National Museum, 103701.

*Remarks*.—Clark's (in Clark and Twitchell, 1915, pl. 27, fig. 2a) original figure of the type specimen of this species showed a small round periproct. Lambert erected *Porobrissus* for this species, distinguishing it from *Nucleopygus* by the shape of its periproct. Cooke (1946, p. 222) later removed the matrix from the sulcus, revealing a longitudinally elongated periproct similar to that found in *Nucleopygus*. Cooke (1955, p. 97) removed the species from *Nucleopygus* because "*Nucleopygus minor* Agassiz, the type species of *Nucleopygus*, appears to have a large, flush periproct." Cooke probably studied Desor's figures of *N. minor* (copied in Mortensen, 1948, fig. 164). Desor's figure does show a flush periproct, but this figure is not correct, as the periproct is definitely not flush, but in a groove (see pl. 24, fig. 10). I agree with Mortensen in considering *E. angustatus* congeneric with *N. minor*. Both species are small, low, with tetrabasal apical system, short, slightly developed petals, supra-marginal, grooved periproct, and single-pored phyllodes.

#### Genus *HYPSOPYGASTER* Bajarunas

*Hypsopygaster* Bajarunas, 1915. *Hypsopygaster*, a new genus of sea-urchins from the Danian deposits of Mangyshlak. Geol. Vestnik-Petrograd, vol. 1, p. 230 (not seen). Type species by monotypy, *Hypsopygaster ungosensis* Bajarunas.

#### GENERIC DESCRIPTION

Small, posterior margin truncated with periproct high on truncation, apical system monobasal, three genital pores, no pore in left anterior genital plate, petals slightly developed, ambulacra single pored beyond petals; bourrelets strongly developed, toothlike; phyllodes single pored, broad with few pores, buccal pores present; adorally tubercles much larger than adapically, naked sternal zone.

*Comparison with other genera*.—*Hypsopygaster ungosensis* resembles *Rhynchopygus marmini* Desmoulins from the Maestrichtian in its small size, slightly developed petals, marginal outline of test, broad phyllodes, pointed bourrelets, and naked pitted zone along interambulacrum 5. *H. ungosensis* differs in having a monobasal apical system with three instead of four genital pores, a longitudinal peri-

proct instead of transverse, a test highly inflated at its posterior margin, and no inner pores in its phyllodes.

*Hypsopygaster* resembles *Nucleopygus* in its small test, inconspicuous petals, and slightly developed phyllodes, but differs in having a marginal periproct, a monobasal apical system with only three genital pores, and strongly developed bourrelets.

Mortensen (1948, pp. 233, 236) considered *Hypsopygaster* as a synonym of *Studeria* mainly because *H. ungosensis* also has only three genital pores. However, the type species of *Studeria*, *S. elegans*, is a larger form, has no inflated posterior, has much more developed petals, and lacks pointed bourrelets.

*Range and distribution*.—Danian of Russia.

#### DESCRIPTION OF TYPE SPECIES

##### **HYPSOPYGASTER UNGOSENSIS** Bajarunas

Plate 25, figures 8-10; plate 26, figures 1, 2; text figures 143, 147

*Hypsopygaster ungosensis* Bajarunas, op. cit., p. 230 (not seen).

*Material*.—Twelve specimens studied from the Geological Museum of the Academy of Sciences at Leningrad; some of them are paratypes.

*Shape*.—Small, average length 12 mm., elongate, posterior margin truncated producing an oblique face sloping outward causing a dorsal overhang; greatest width at center, greatest height near posterior margin at top of posterior truncation.

*Apical system*.—Anterior (text fig. 147), monobasal, three genital pores, left anterior pore absent, ocular plates very small.

*Ambulacra*.—Petals subpetaloid, not visible on unweathered specimens, pores of pore pair equal, not conjugate; petals short, equal in length, extending one-half distance to margin (text fig. 147), open, interporiferous zone less than twice width of poriferous zone; five to seven pore pairs in each poriferous zone; ambulacral plates single pored beyond petals.

*Periproct*.—High on posterior truncation, slightly visible from above on some specimens, longitudinal, slight groove below opening.

*Peristome*.—Anterior, higher than wide, sunken.

*Floscelle*.—Bourrelets strongly developed, pointed, extending out over peristome opening; phyllodes (text fig. 143) sunken, broad, single pored, arranged in one series in each half-ambulacrum, three or four pores in each; buccal pores separated from peristome by rim joining bourrelets; sphaeridia in a double series along midline.

*Tuberculation*.—Adorally tubercles considerably larger than adapically; naked, pitted medial zone in interambulacrum 5.

*Occurrence*.—Danian, Ungozya, Mangyshlak, Russia.

*Location of type specimen*.—Geological Museum of the Academy of Sciences, Leningrad, Russia.

#### Genus *OCHETES* Pomel

*Ochetes* Pomel, 1883. Class. méth., p. 57. Type species, herein designated, *Nucleolites morrisii* Forbes.

#### GENERIC DESCRIPTION

Small, elongate, low; apical system tetrabasal, central, four genital pores; petals slightly developed, periproct supramarginal, in deep groove; peristome anterior, pentagonal; bourrelets well developed; phyllodes very broad, double pored with pore pairs in two series, few in inner series; no buccal pores, sphaeridia in two rows in each ambulacrum; tubercles on adoral surface large with bosses eccentric anteriorly in large scrobicules; naked, pitted area in interambulacrum 5, ambulacrum III.

*Comparison with other genera*.—*Ochetes* is distinguished from *Nucleopygus* by its less developed petals, more developed bourrelets, broader, double-pored phyllodes lacking buccal pores, and much larger adoral tubercles. It is easily distinguished from *Nucleolites* by its lower test, subpetaloid petals, more developed bourrelets, and greatly widened phyllodes with fewer pore pairs in the inner series. Furthermore, in *Ochetes morrisii* the tubercles on the adoral surface are much larger than those on the adapical, and there is a naked, pitted area in interambulacrum 5 and ambulacrum III.

*Ochetes* is similar to *Rhynchopygus*, both genera having small, low tests, slightly developed petals, tetrabasal apical systems, supramarginal periproct, and a well-developed floscelle. In both genera the tubercles on the adoral surface are large, and there is a naked, pitted area in interambulacrum 5 and ambulacrum III. However, in *Ochetes* the phyllodes are double pored, whereas in *Rhynchopygus* they are single, and in *Ochetes* the bourrelets are less pointed. As both these distinguishing characters are more primitive, and as *Ochetes* occurs in older rocks, it is probably an ancestor of *Rhynchopygus*.

*Remarks*.—Lambert and Thiéry (1921, p. 347) and Mortensen (1948, p. 185) both considered *Ochetes* a synonym of *Nucleopygus*. While it is true that most of the species that Pomel referred to his

genus probably do belong to *Nucleopygus*, one of them, Forbes' *Nuculolites morrisii*, definitely does not. Unfortunately, this species had never been well figured, and the characters that distinguish it from *Nucleopygus* were not known to Lambert and Thiéry, Mortensen, or Pomel.

*Range and distribution.*—Lower Cretaceous (Albian–Cenomanian), England.

#### OCHETES MORRISII (Forbes)

Plate 25, figures 5-7; text figures 144-146

*Nuculolites morrisii* Forbes, 1849. Mem. Geol. Surv. United Kingdom, dec. 1, p. 8.

*Material.*—I studied 11 specimens of this species in the British Museum (Natural History) including the specimen figured by Wright (1882, pl. 78, fig. 4). All the specimens came from the same two localities mentioned by Forbes in his original description of the species. The single specimen from Blackdown, Devon, is silicified, but the other specimens, all from Warminster, Wiltshire, are calcareous.

*Shape.*—Small, largest specimen 16.5 mm. long, elongate, angular marginal outline, posterior pointed except where blunted by anal groove, sides straight, parallel, very depressed, with greatest height posterior to center; adorally depressed, interambulacrum 5 slightly inflated along median suture.

*Apical system.*—Central, tetrabasal, most sutures not visible, genital plate 2 small (text fig. 144) not extending posteriorly between posterior genital plates; four genital pores, right posterior pore slightly displaced laterally and posteriorly; ocular plates narrow, long.

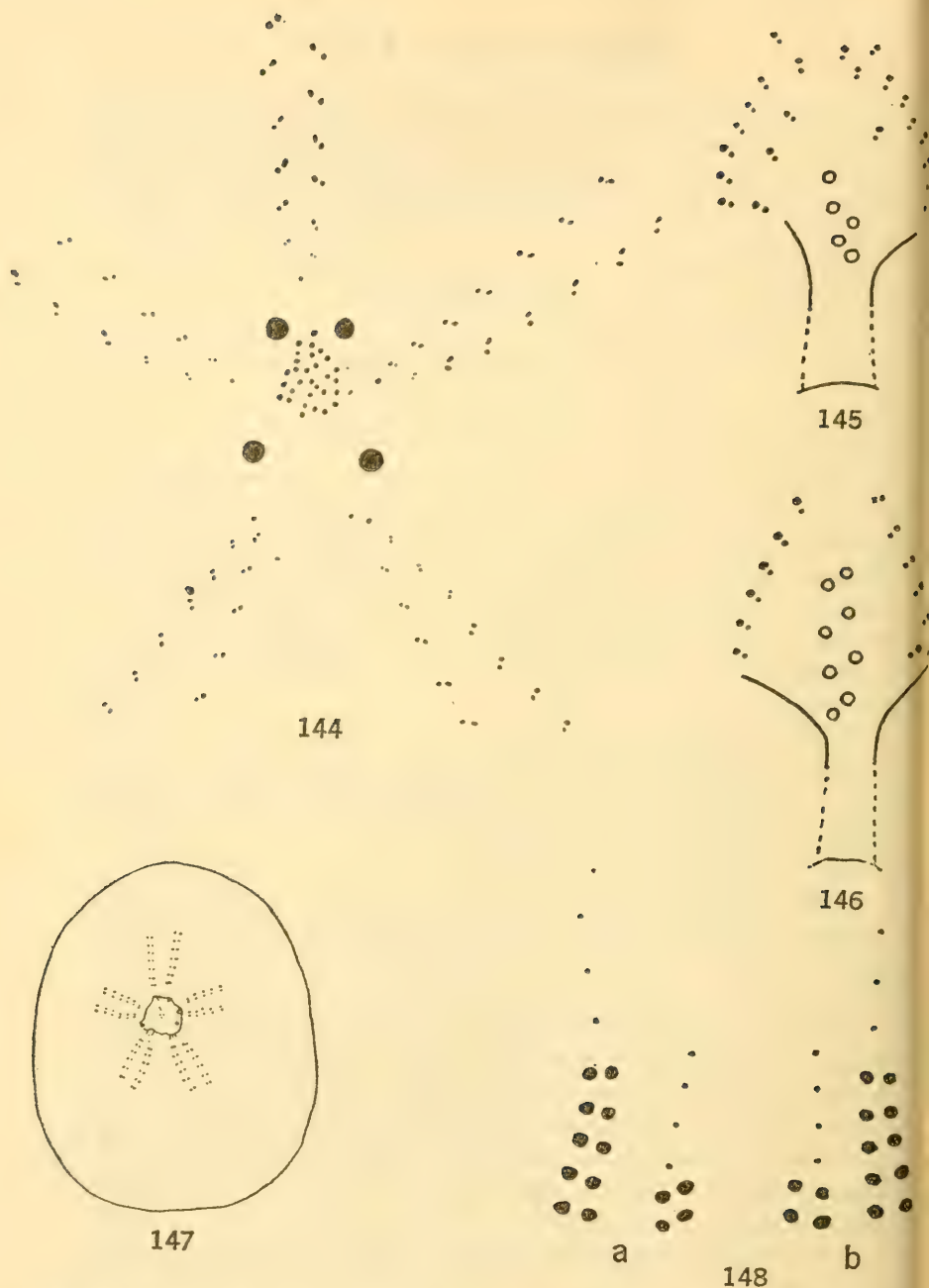
*Ambulacra.*—Petals only slightly developed, very narrow, not closing, extending almost to margin, petals II, III, and IV straight, petals V and I flexuous, curving distally away from each other. Interporiferous zones expanding distally; poriferous zones narrow, pores oblique to each other, inner pore distal to outer, not conjugate, slightly elongated obliquely, inner round (text fig. 144); pores beyond petals minute.

*Adoral interambulacra.*—Plates large, not alternating, single plate at peristome.

*Periproct.*—Supramarginal, midway between apical system and posterior margin; circular to oval, in deep, flat-bottomed, triangular groove extending to posterior margin.

*Peristome.*—Anterior, higher than wide, pentagonal.





FIGS. 144-148.—144-146, *Ochetes morrisii* (Forbes): 144, Portion of adapical region in specimen E 42411 in the British Museum (Natural History), from the Lower Cretaceous (Upper Albian) Upper Greensand, Warminster, Wiltshire, England,  $\times 10$ . 145, 146, Phyllodes of ambulacra I and III of specimen E 32388 from the same locality,  $\times 20$ . 147, *Hypsopygaster ungosensis* Bajarunas: Adapical view of specimen in Geologic Museum of RAN, Russia, from the Danian, at Ungozya, Mangyshlak, Russia,  $\times 4$ . 148, *Cassidulus cariboeorum* Lamarck: a, View of distal portion of petal as viewed from the outside of the test of USNM 634001b, from Antigua West Indies (living),  $\times 11$ ; b, inside view of same petal of same specimen.

*Floscelle*.—Bourrelets well developed, triangular, not vertical. Phyllodes very broad, double pored (text figs. 145, 146), two series of pore pairs in each half-ambulacrum; few in inner series, one in ambulacrum III, one or two in ambulacra II and IV, one to three in ambulacra V and I: five to eight in each outer series, all pores widely separated from peristome. Sphaeridia very large, approximately eight in each ambulacrum, arranged in double alternating series; no buccal pores.

*Tuberculation*.—Tubercles, perforate, very small adapically, adorally much larger, with deep, large, longitudinally oriented scrobicules, with bosses anteriorly situated in each scrobicule; tubercles largest in paired interambulacra midway between peristome and margin, no tubercles in ambulacrum III, or in anterior portion of interambulacrum 5. All adoral areas devoid of tubercles, profusely pitted.

*Occurrence*.—Cretaceous, Upper Albion, Upper Greensand, Blackdown, Devon, Warminster, Wiltshire; Cenomanian, Chloritic marl, Chardstock, Somerset.

*Location of type specimen*.—Unknown; not in the British Museum (Natural History). According to Wright (1875, Cretaceous, p. 251), Forbes "detected" the type in Professor Tennant's Collection.

*Remarks*.—d'Orbigny (1858, p. 407) described and figured a French specimen that he referred to this species. I have not seen his specimen, but from a study of his figures and his description of it, it does not belong to this species. d'Orbigny's specimen is much larger and has a very different shape, with its greatest width posterior to the center, whereas in the English specimens of *Ochetes morrisii* the sides are parallel. The test is much higher in the French specimen, and the margin much smoother, with an anteriorly eccentric instead of central apical system, much more developed petals, with petals V and I straight instead of curved marginally. Adorally, the French specimen lacks the well-developed floscelle, naked, pitted areas in interambulacrum 5 and ambulacrum III, and the large, deeply scrobiculated tubercles. This specimen is certainly not conspecific or even congeneric with the English specimens. Although it may represent a new species, I do not erect one myself, as I have not seen any specimens.

*Morphological note*.—Owing to the severe weathering of some of the specimens of *O. morrisii*, the phyllodes appear at first glance to be single pored. The pores have been so enlarged that the calcite separating the two pores of a pore pair is usually absent.

Genus *CASSIDULUS* Lamarck

*Cassidulus* Lamarck, 1801. *Système animaux sans vertèbres*, p. 348. Type species by monotypy, *Cassidulus cariboeorum* Lamarck.

Synonym: *Glossaster* Lambert.

## GENERIC DESCRIPTION

Small, low, elongate; apical system monobasal, four genital pores; petals slightly or well developed, straight, open or closing distally, poriferous zones of same petal usually unequal, ambulacral plates beyond petals single pored; periproct supramarginal, longitudinal or transverse, with groove extending from opening to posterior margin; peristome anterior, pentagonal, transverse; bourrelets well developed; phyllodes widened, single pored with slight crowding of pores, one or two or no occluded pores; buccal pores present; adorally, tubercles much larger, scrobicules often polygonal, with bosses eccentric anteriorly; adorally, naked, often pitted area in interambulacrum 5, ambulacrum III.

*Comparison with other genera.*—*Cassidulus* is very similar to *Rhynchopygus* but differs in having a monobasal apical system as opposed to the tetrabasal system in *Rhynchopygus*. As *Cassidulus* occurs later, in the Tertiary, whereas *Rhynchopygus* is from the Upper Cretaceous, and since *Cassidulus* has a more advanced apical system, there is little doubt that it is descended from *Rhynchopygus*. *Cassidulus* differs from *Rhyncholampas* in having a smaller, more elongate test, narrower, nonlanceolate petals, a usually less posterior periproct, and phyllodes with fewer pores. It differs from *Hypsopygaster* in having more developed petals and less pointed bourrelets.

*Remarks.*—This genus includes most of the Tertiary species that Lambert and Thiéry referred to their *Procassidulus*, except for Twitchell's *Cassidulus depressus*, which Cooke (1959, p. 64) considers a synonym of *Eurhodia patelliformis* (Bouve), Desor's *Cassidulus amygdala*, which also appears to be a *Eurhodia*, and Kew's *Cassidulus mexicanus*, which is a *Rhyncholampas*. Many of the pre-Tertiary species that Lambert and Thiéry refer to *Procassidulus*, including the type species, have a tetrabasal apical system and should be referred to *Rhynchopygus*. All the Tertiary species that they refer to *Rhynchopygus*, except *R. dyasteroides* Duncan, have monobasal apical systems and should be referred to *Cassidulus*. Cooke (1959, pp. 56-59) refers four species to *Cassidulus* (*Cassidulus*), but three of them, *C. sabistonensis* Kellum, *C. gouldii* (Bouve), and *C. ericsoni* Fischer, are very large, have well-developed phyllodes, and probably

should be referred to *Rhyncholampas*. The fourth, *C. trojanus*, is small but has more developed phyllodes than are usually found in *Cassidulus*. This species, like several others, has characters of both *Cassidulus* and *Rhyncholampas* and cannot be referred definitely to either. These intermediate forms blur the distinction between the two genera.

There are three American west coast species that belong to *Cassidulus*: *C. ellipticus* Kew, *C. californicus* Anderson, and *C. ynezensis* Kew. I have studied all the type specimens of these species, which are in the Museum of Paleontology at Berkeley, Calif. The two cotypes of *Cassidulus ellipticus* Kew are both poorly preserved, but the specimen figured in Kew's (1920) plate 39, figure 3a, c, d, shows the adapical surface and is herein designated the lectotype. The phyllodes are not visible on either of these specimens, but from the small size of the low and very elongated test, supramarginal, transverse periproct, and monobasal apical system this species should be referred to *Cassidulus*. The neotype of *Cassidulus californicus* Anderson also should be referred to *Cassidulus*. Although the specimen is poorly preserved, enough of one of the phyllodes is visible to see that it is very simple, with only one pore occluded in each half-ambulacrum. The test is small and elongate, and the apical system is monobasal. The specimen figured by Grant and Hertlein (1938, pl. 4, fig. 7; pl. 30, fig. 7) is wrongly referred by them to *C. californicus*. It differs from the latter in having a much larger, more inflated test, strongly lanceolate petals with more unequal poriferous zones in each petal, more anterior apical system, more marginal periproct lacking an adapical overhang, a less depressed peristome, and less developed bourrelets. Apparently it is a new species of *Rhyncholampas*.

Kew's *Cassidulus ynezensis* is represented by one very poorly preserved specimen which is slightly crushed, with a large part of the adapical surface missing, and so badly weathered that no details are discernible of the phyllodes. Kew referred this species to *Rhynchopygus*, but since it has a monobasal apical system, it is a *Cassidulus*. Grant and Hertlein (1938, p. 109) consider *C. ynezensis* as a synonym of *C. californicus*, but the two species are quite distinct. *C. ynezensis* is larger, lower, with sharper margin, smaller peristome, and narrower petals.

*Range and distribution.*—Eocene to Recent of worldwide distribution.



## DESCRIPTION OF TYPE SPECIES

**CASSIDULUS CARIBOEARUM** Lamarck

Plate 26, figures 3-7; text figures 148-150

*Cassidulus cariboeorum* Lamarck, 1801. *Système animaux sans vertèbres*, p. 349.  
For complete synonymy see Mortensen (1948, p. 205).

*Material*.—Two specimens studied from the Museum of Comparative Zoology at Harvard, and three from the U. S. National Museum.

*Shape*.—Small, largest specimen 31 mm. long, elongate, anterior margin smoothly rounded, or slightly blunted posterior slightly truncated by anal groove, sides expanding slightly posteriorly with greatest width posterior to center. Adapical surface inflated with greatest height anterior at apical system; adoral surface flat.

*Apical system*.—Anterior, monobasal, with four genital pores; according to Mortensen (1948, p. 207) genital pores first appear in specimens approximately 13 mm. long.

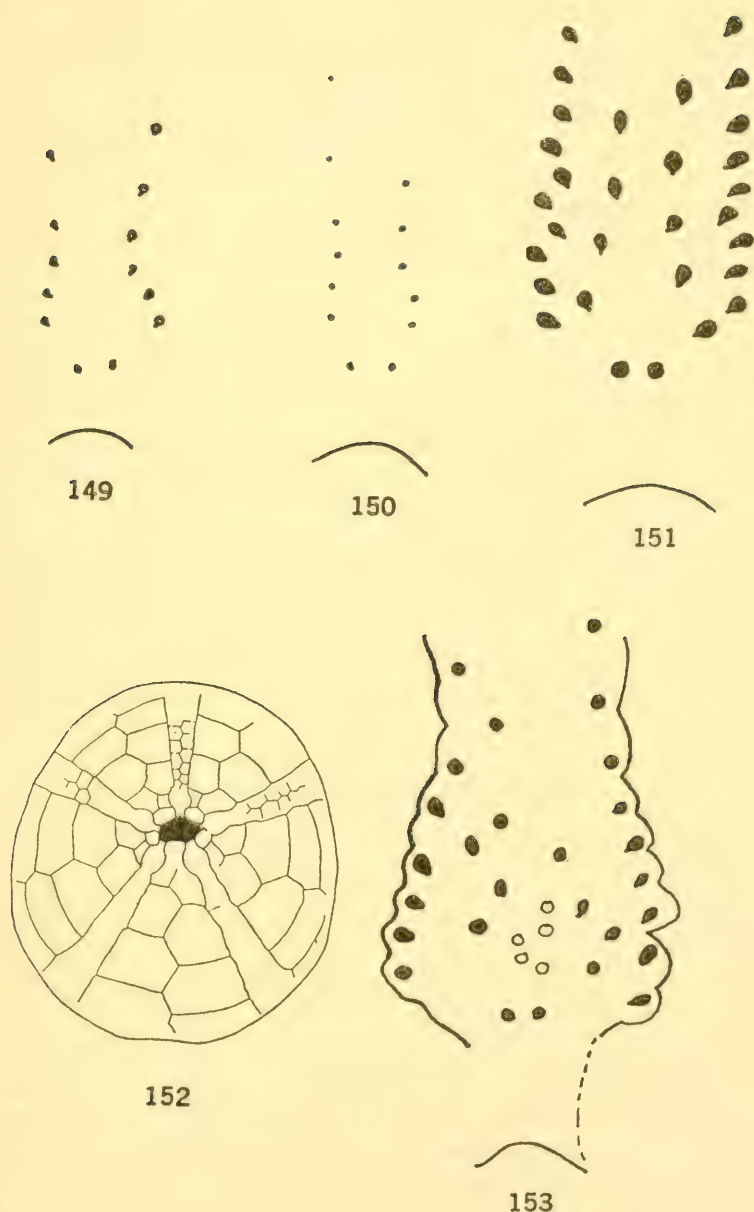
*Ambulacra*.—Petals approximately equal length, broad, slightly closing distally. Interporiferous zones more than twice width of poriferous zones, tapering slightly distally; poriferous zones narrow, outer pore larger than inner, slightly elongated transversely; inner pore round, pores slightly conjugate (see pl. 26, fig. 6). Poriferous zones unequal in length; in petals V and I from three to seven more pore pairs in outer series than inner; usually equal in petals II and III, but in petal IV usually three more pore pairs in posterior series than in anterior. Pores in ambulacral plates beyond petals very small, single pore in each plate; on exterior of test often in line with outer pore of poriferous series (text fig. 148a), but on interior of test always in line with inner series of pores (text fig. 148b).

*Periproct*.—Supramarginal, transverse, two-thirds to four-fifths distance from apical system to posterior margin, opening rounded dorsally, pointed ventrally, overhung slightly by adapical surface; flat groove equal in width to opening, extending to posterior margin.

*Peristome*.—Large, pentagonal, transverse, anterior.

*Floscelle*.—Bourrelets well developed, inflated, vertically sided. Phyllodes (text fig. 149) single pored, widened, pores in single series except in few instances where one pore displaced out of series, almost occluded; approximately four to six pores in each series, pores large; viewed from inside of test, pores in straighter line (text fig. 150) with less widening of phyllodes. Buccal pores present.

*Tuberculation*.—Tubercles with small perforate mamelons, large vertical bosses. Adapically, tubercles small, with circular scrobicules;



FIGS. 149-153.—149, 150, *Cassidulus cariboeorum* Lamarck: 149, Phyllode of ambulacrum I viewed from the outside of USNM 634001, from Antigua, West Indies (living),  $\times 13$ ; 150, view from inside of same phyllode. 151, 152, *Rhyncholampas grignonensis* (DeFrance): 151, Phyllode of USNM 633997, from the Middle Eocene, at Cahaigues (Eure), France,  $\times 15$ ; 152, adoral view of same specimen showing plate arrangement,  $\times 1$ . 153, *Rhyncholampas ellipticus* (Arnold and Clark): Phyllode of ambulacrum III of holotype, 3284, in the Museum of Comparative Zoology, Harvard, from the Eocene, western side of hills east of Montpelier, St. James Parish, Jamaica,  $\times 15$ .

adorally, tubercles much larger, with polygonal scrobicules, with bosses eccentric anteriorly, naked, pitted area in median of interambulacrum 5, ambulacrum III, and edge of adjacent interambulacra.

*Occurrence*.—Recent of West Indies.

*Habitat*.—Mortensen (1948, p. 209) suggests that the species lives buried in coarse sand.

*Location of type specimen*.—Unknown; not found by this author in the Lamarck Collection at the Muséum d'Histoire Naturelle, Genève, Switzerland.

#### Synonym of *CASSIDULUS*

*Glossaster* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 55, p. 39. Type species by original designation, *Cassidulus sorigneti* Cotteau (1887, p. 512).

*Remarks*.—Lambert established *Glossaster* as a subgenus of *Pro-cassidulus*, differentiating it from the latter by its subtriangular peristome. Unfortunately, I was unable to find any specimens of this species in the Paris museums, but from Cotteau's figures it looks like a typical *Cassidulus* having a small, low test, obliquely truncated for the supramarginal periproct, flat adoral surface with well-developed bourrelets, naked medial zone adorally, and short petals. The fact that the periproct is subtriangular does not seem of sufficient importance to warrant subgeneric distinction, as the shape of the periproct is quite variable within species of *Cassidulus*.

#### Genus *RHYNCHOLAMPAS* A. Agassiz

*Rhyncholampas* A. Agassiz, 1869. Bull. Mus. Comp. Zool., vol. 1, p. 270. Type species by subsequent designation, Lambert (1918, p. 41), *Pygorhynchus pacificus* A. Agassiz.

Synonyms: *Anisopetalus* Arnold and Clark; *Galerolampas* Cotteau; ? *Gisopygus* Gauthier; *Plagiopygus* Lambert.

#### GENERIC DESCRIPTION

Medium to large, elongate, oval or with greatest width posterior to center, moderately to highly inflated; apical system anterior, monobasal; petals lanceolate, equal, closing, with unequal poriferous zones; ambulacra single pored beyond petals; periproct slightly supramarginal, marginal or slightly inframarginal, transverse; peristome anterior, pentagonal, wider than high; bourrelets moderately developed; phyllodes single pored, widened, usually with two series of pores in each half-ambulacrum, approximately four pores in each inner series; in some species three series of pores in each half-

ambulacrum; buccal pores present; tubercles on adoral surface much larger than on adapical, scrobicules large, bosses eccentric anterior; naked, often pitted area in interambulacrum 5, ambulacrum III.

*Comparison with other genera.*—*Rhyncholampas* is distinguished from *Cassidulus* by its larger test, broader, lanceolate petals, generally more posterior periproct, and more developed phyllodes with more occluded pores. Although the type species of these two genera are very distinct from one another, there are species which have some of the characters of both and are difficult to place definitely in one of them.

*Remarks.*—Mortensen (1948, p. 202) incorrectly states that when A. Agassiz established this genus he made *Cassidulus cariboeorum* the type species. Furthermore, Grant and Hertlein (1938, p. 107) are mistaken in saying that *C. cariboeorum* is the type species by monotypy. Agassiz referred two species to his genus, *C. cariboeorum* and *R. pacificus*, but did not select a type species. Lambert and Thiéry designated *R. pacificus*. Mortensen says that even if *R. pacificus* were considered as the type species of *Rhyncholampas*, the genus would still be a synonym of *Cassidulus*. He states that *R. pacificus* has more developed phyllodes and that the pores in its petals are more unequal, but suggests that these differences may be due to the different size of the specimens examined, and that if specimens of the same size were compared, these differences might be so small as to be unimportant for a generic distinction. This argument would be pertinent if the species *C. cariboeorum* were based on immature specimens, and *R. pacificus* on adults. Such is not the case. Many specimens of *C. cariboeorum* are known, and none are larger than 31 mm. in length. There is no evidence that these small specimens are not adults. Fortunately, there are two small specimens of *R. pacificus* in the U. S. National Museum, one 21 mm. long and the other 35 mm., and these immature specimens are generically distinct from *C. cariboeorum*. A phyllode in the smallest specimen already has three occluded pores (text fig. 154) in each half-ambulacrum, whereas no occluded pores occur in specimens of the same size or even larger of *C. cariboeorum*. It is true that the pores in the petals of the small specimen of *R. pacificus* are more equal, with the outer pore less elongated (pl. 28, fig. 1) than the outer pore in an adult. However, the shape of the petals in *R. pacificus* is quite different from the petals in *C. cariboeorum*. In *R. pacificus* the petals are lanceolate with more of a tendency to close distally. This difference is evident even on the smallest specimen.



*Range and distribution.*—Paleocene to Recent, of worldwide distribution. There are many species from the Cenozoic of eastern United States which Cooke has referred to *Plagiopygus* (which he considers a subgenus of *Cassidulus*) or *Cassidulus* (*Cassidulus*), which probably should be referred to *Rhyncholampas*, including *R. sabistonensis* Kellum, *R. gouldii* (Bouve), *R. ericsoni* (Conrad), *R. alabamensis* (Twitchell), and *R. georgiensis* (Twitchell). Kew's west coast species *Cassidulus* (*Rhynchopygus*) *mexicanus* is very large, with well-developed broad lanceolate petals, and should be referred to *Rhyncholampas*. Unfortunately, on the holotype, and evidently the only specimen known of this species, the adoral surface is destroyed and nothing is known of the phyllodes. A photograph of the adapical surface is included herein on plate 29, figure 4. This species is quite similar to *R. evergladensis* (Mansfield) from southeastern United States, also from the Late Miocene of Florida. Its phyllodes are probably similar to the very well developed phyllodes in *R. evergladensis*.

#### DESCRIPTION OF TYPE SPECIES

##### RHYNCHOLAMPAS PACIFICUS (A. Agassiz)

Plate 27, figures 5-8; plate 28, figures 1-3; text figures 154-159

*Pygorhynchus pacificus* A. Agassiz, 1863. Bull. Mus. Comp. Zool., vol. 1, p. 27.

*Remarks.*—Mortensen (1948, p. 210) gives a very thorough description of this species, and it is not necessary to redescribe it here, but new photographs are included. Although there are only four specimens in the collections of the U. S. National Museum, they vary in size from 8.5 to 55 mm. and exhibit some interesting ontogenetic changes described below. The smallest specimen is the smallest that has ever been described.

#### ONTOGENY

*Apical system.*—On the smallest specimen (text fig. 159), 8.5 mm. long, there are no genital pores, but four gonoducts are visible on the inside of the test in interambulacra 1, 2, 3, and 4, near the apical system. There are approximately 11 madreporic pores, and only 1 tubercle. There are still no genital pores in the specimen 21 mm. long (text fig. 158), but there are many more tubercles and madreporic pores. In the specimen 35 mm. long (text fig. 157), genital pores are present.



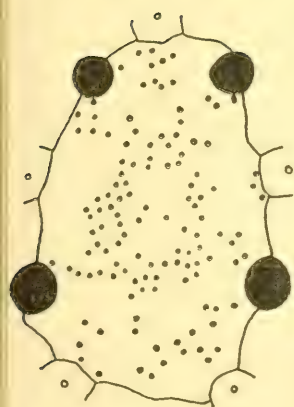
154



155



156



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158



159

FIGS. 154-159.—Growth changes in the phyllodes and apical system of *Rhyncholampas pacificus* (A. Agassiz): 154, USNM 6988, from Cape St. Lucas, Xantus; 155, USNM 32907, from Pescadero Point, Lower California; 156, USNM 3561, from Acapulco, Mexico; all of phyllode II,  $\times 10$ ; 157, USNM 32907; 158, USNM 6988; 159, USNM 929, from Albatross station 2995,  $\times 20$ .

*Ambulacra*.—In the smallest specimen, the petals are short, extending less than one-half the distance from the apical system to the margin. In petal III there are 11 pore pairs in the left poriferous zone, and 1 less in the right; in petals II and IV, 11 in the posterior poriferous zones with 4 less in the anterior; in petals I and V, 14 in the outside zones with 6 less in the inside. Because of the few pore pairs in the petals, this difference in the number of pore pairs in the poriferous zones of the same petal is very marked. In the larger specimens, although the difference in the number of pore pairs remains approximately the same, it is less marked because of the greater length of the petals. Pore pairs are added continuously throughout the growth of the echinoid but at a slightly decreasing rate. In the specimen 21 mm. long there are 25 pore pairs in ambulacra III, in specimen 35 mm. long there are 36, and in a specimen 55 mm. long there are 43. The plotting of these points on a graph produces a curve very similar to that found in an ontogenetic study (Kier, 1957, p. 853) of *Echino-lampas fraasi* De Loriol. The projection of this curve indicates that the first pore pairs are probably introduced in individuals between 3 and 4 mm. long. Since there are more pore pairs in the outside poriferous zones of ambulacra I and V, they would first occur in these zones. The difference in the number of pore pairs in the poriferous zones in the same petal is fairly consistent in all the specimens, with 1 more in the left zone of petal III, except in one specimen in which there is 1 more in the right; 2 to 4 more in the posterior zones of petals II and IV, except for one specimen in which there is 1 less pore pair in the posterior zone of petal II; and 6 to 7 more in the outside zones of petals I and V.

The shape of the pores changes with growth. In the smallest specimen, 8.5 mm. long, the pores are equal, both being round. Mortensen (1948, p. 211) says of a specimen 12 mm. long that the outer and inner pores "are, of course, not conjugate." However, in this specimen which is even smaller than his, there is a definite conjugation groove joining the pores in the petals. In the specimen 21 mm. long (pl. 28, fig. 1) the pores of a pair are no longer equal as the outer pore is elongated transversely. In the specimens 35 mm. long (pl. 28, fig. 2) and 55 mm. long (pl. 28, fig. 3) the outer pores are increasingly more elongated and the conjugation groove more marked.

*Periproct*.—On the smallest specimen, the periproct is situated less posteriorly than on the larger, being less than two-thirds the distance from the apical system to the posterior margin, whereas on the largest

specimen it is almost on the posterior margin. Furthermore, on the smallest specimen the periproct is higher, with an oblique opening, as opposed to the almost vertical opening in the larger specimens, and the opening is larger relative to the size of the test, the width of the opening being 21 percent of the length of the test in the smallest specimen but only 15 percent in the largest.

*Floscelle*.—In the smallest specimen the bourrelets are slightly developed, with the result that the peristome is oval transversely and not subpentagonally angular as in the larger specimen. The phyllodes are very slightly developed, with no widening and with only slight crowding of the pores, with only one or two pores slightly displaced from each series. In the specimen (text fig. 154) 21 mm. long, in ambulacrum II the pores are much more crowded, with three pores occluded in each series, on the specimen 35 mm. long (text fig. 155) four pores are occluded, and on the specimen 55 mm. long there are six (text fig. 156). The phyllodes also increase relatively in width.

*Tuberculation*.—It is particularly interesting to note that the tubercles in the smallest specimen are approximately the same size as they are in the largest. There is very little growth in a particular tubercle as the echinoid grows. Accordingly, the tubercles on the smallest specimen are very large relative to the size of the test. Presumably the spines would be very large on the smallest specimen also, but not enough spines are preserved on this specimen to be certain.

*Habitat*.—According to A. Agassiz (1873, p. 555), this species lives on sandy beaches, from 5 to 6 feet below low-water mark, half buried in the sand up to the extremity of its petals.

*Occurrence*.—Recent of American west coast.

*Location of type specimen*.—Museum of Comparative Zoology, Harvard.

#### Synonym of RHYNCHOLAMPAS

*Anisopetalus* Arnold and Clark, 1927. Mem. Mus. Comp. Zool., vol. 50, No. 1, p. 44. Type species by original designation, *Anisopetalus ellipticus* Arnold and Clark.

#### DESCRIPTION OF TYPE SPECIES

##### RHYNCHOLAMPAS ELLIPTICUS (Arnold and Clark)

Plate 29, figures 1-3; text figure 153

*Anisopetalus ellipticus* Arnold and Clark, 1927. Mem. Mus. Comp. Zool., vol. 50, p. 45, pl. 6, figs. 16-20.

*Material*.—The holotype and six other specimens were studied.

*Shape*.—Medium size, holotype 50 mm. long, elongate, with



smoothly rounded anterior margin, slightly truncated posterior; low, with gently sloping sides, adoral surface flat.

*Apical system*.—Anterior, monobasal.

*Ambulacra*.—Petals broad, of equal length, closing distally. Poriferous zones narrow, of unequal length in holotype: six more pore pairs in right poriferous zone in petal III than in left, two more in posterior poriferous zones of petals II and IV than in anterior zones, and approximately five more in outer poriferous zones of petals V and I. Pores conjugate, outer pore slightly elongated transversely, inner pore round. Interporiferous zones wide, almost three times as wide as poriferous zones, tapering distally.

*Periproct*.—Marginal to slightly supramarginal, transverse.

*Peristome*.—Anterior, small, pentagonal, transverse.

*Floscelle*.—Bourrelets well developed, vertical, inflated. Phyllodes (text fig. 153) single pored, pores arranged in two series in each half-ambulacrum; approximately eight in each outer series, four or five in each inner. Sphaeridia pits in two rows along midline of ambulacrum. Buccal pores present.

*Tuberculation*.—Adorally, tubercles larger, with naked, slightly pitted area in interambulacrum 5 and ambulacrum III.

*Occurrence*.—Eocene, western side of hills east of Montpelier, St. James Parish, Jamaica.

*Location of type specimen*.—Museum of Comparative Zoology, Harvard, No. 3284.

*Remarks*.—Arnold and Clark distinguished their genus from *Cassidulus* on the grounds that the petals in *Anisopetalus* have poriferous zones of unequal length. However, as pointed out by Cooke (1959, p. 59) the poriferous zones in *Cassidulus* are also unequal. *R. ellipticus* is very similar to species of *Rhyncholampas*, and *Anisopetalus* is herein considered a synonym of *Rhyncholampas*. The poriferous zones of its petals are narrower, and its periproct is slightly more posterior, than usually found in *Rhyncholampas*, but these differences do not seem to warrant generic distinction for this species.

Santos' (1958, p. 11) *Anisopetalus oliveirai* from the Miocene of Brazil is an *Echinolampas* (see p. 107).

#### Synonym of RHYNCHOLAMPAS

*Galerolampas* Cotteau, 1889. Pal. franc., Tert., Échinides Éocènes, vol. 2, p. 1.

Type species by monotypy, *Galerolampas sorigneti* Cotteau (op. cit., p. 3).

*Remarks*.—Lambert and Thiéry (1921, p. 371) considered *Galero-*  
*lampas* as a subgenus of *Rhyncholampas*, and although Mortensen

(1948, p. 246) maintained it as a separate genus, he thought it very similar to *Rhyncholampas*. Unfortunately, I was not able to locate any specimens of the type species in the Paris museums, but from a study of Cotteau's figures and an examination of the holotype of *Rhyncholampas thiéryi* Lambert, a species Lambert and Thiéry considered congeneric with the type species, *Galerolampas* appears to be a synonym of *Rhyncholampas*. It has the same petal arrangement, similar shape, transverse pentagonal peristome, well-developed floscelle, and naked medial zone in interambulacrum 5 and ambulacrum III typical of *Rhyncholampas*. It differs only in having a slightly inframarginal periproct, whereas in most species of *Rhyncholampas* the periproct is either marginal or slightly supramarginal. This difference does not seem of sufficient importance to warrant generic distinction.

#### ? Synonym of RHYNCHOLAMPAS

*Gisopygus* Gauthier, in Fourtau, 1899. Mém. Inst. Égypt., vol. 3, p. 648. Type species, *Rhynchopygus navillei* De Loriol, by subsequent designation, Lambert and Thiéry (1921, p. 365).

*Remarks*.—I have not seen any specimens of the type species of this genus. As no drawings have ever been published of the structure of the phyllodes, it is not possible to know for certain the generic affinities of this genus. Both Lambert and Thiéry (1921, p. 365) and Mortensen (1948, p. 252) considered this genus a synonym of *Eurhodia*. Its test, however, is not as elongate nor its adoral surface as flat as in *Eurhodia*. It seems very similar to *Rhyncholampas*, and is herein considered provisionally as a synonym of it.

#### Synonym of RHYNCHOLAMPAS

*Plagiopygus* Lambert, 1898. Bull. Soc. Belge Géol., ser. 2, vol. 11, p. 162. Type species by original designation, *Nucleolites grignonensis* DeFrance. Lambert and Thiéry (in Lambert, 1913) proposed a substitute name, *Pleuropygus* for *Plagiopygus*, considering the latter to be preoccupied by *Plagiopyga* Boheman, 1848. However, since the names are not exactly the same, Lambert's *Plagiopygus* can be maintained, and *Pleuropygus* is a junior objective synonym of *Plagiopygus*.

#### DESCRIPTION OF TYPE SPECIES

##### RHYNCHOLAMPAS GRIGNONENSIS (DeFrance)

Plate 28, figures 4-8; text figures 151, 152

*Nucleolites grignonensis* DeFrance, 1825. Dict. sci. nat., vol. 35, p. 214.

*Material*.—Two specimens studied in the collections of the U. S. National Museum, and several, including Cotteau's figured specimen, in the École National Supérieure des Mines, Paris.

*Shape*.—Medium size, oval, inflated, greatest width and height posterior to center; margin gently rounded except for slight posterior truncation, peristome depressed.

*Apical system*.—Anterior, monobasal, madreporite inflated.

*Ambulacra*.—Petals narrow, petal III shorter than others, II and IV extending over two-thirds distance to margin; petals V and I over one-half distance; interporiferous zones over twice width poriferous zone; petals closing distally; poriferous zones depressed, of unequal length: one more pore pair in right zone of petal III, two more in posterior zones of petals II and IV, six more in outside zones of petals I and V; this character variable with specimens; pores conjugate, outer pore elongate transversely, inner smaller and round.

*Adoral interambulacra*.—Single plate (text fig. 152) at peristome, preceded by two alternating plates, one much larger than the other in interambulacrum 3, smaller plate adjacent to ambulacrum III; in interambulacra 1 and 4 smaller plate adjacent to ambulacra I and V respectively; in interambulacrum 5 adjacent to ambulacrum I; plates preceding these regularly alternating, of approximately equal size.

*Periproct*.—Marginal to slightly supramarginal; transverse with slight groove at adoral side of opening.

*Peristome*.—Anterior, depressed, pentagonal.

*Floscelle*.—Bourrelets well developed (pl. 28, fig. 8); vertically sided. Phyllodes (text fig. 151) widened single pored, two series in each half-ambulacrum: seven or eight pores in each outer series, four to five in each inner series; buccal pores, sphaeridia present.

*Tuberculation*.—Adorally, tubercles larger; naked median band in interambulacrum 5, short length at ambulacrum III.

*Occurrence*.—Middle Eocene of France.

*Location of type specimen*.—According to Lambert and Jeannet (1928, p. 126) the type is in the École National Supérieure des Mines.

*Remarks*.—Lambert erected this genus for all the Tertiary species of *Pygorhynchus*. Later, he (Lambert and Thiéry, 1921, p. 370) placed his genus in synonymy with *Rhyncholampas*. Mortensen (1948, p. 203) considered it, along with *Rhyncholampas*, as a synonym of *Cassidulus*. Cooke (1959, p. 59) maintained *Plagiopygus* as a subgenus of *Cassidulus*, distinguishing it from the latter by its more terminal periproct, and more inflated posterior extremity.

The type species of *Plagiopygus* is quite similar to the type species of *Rhyncholampas* and certainly congeneric with it. Both species have approximately the same shape, similar petals, although slightly more lanceolate in *R. pacificus*, transverse periproct and peristome,



very similar floscelle, and a naked band in interambulacrum 5 and ambulacrum III.

### CLYPEOLAMPADIDAE Kier, new family

Large, highly inflated, flat adoral surface, elongate; apical system anterior, tetrabasal or monobasal; petals broad, straight, open, long, with pores joined by deep conjugation groove, poriferous zones in same petal of equal length, ambulacral plates beyond petals single pored; periproct inframarginal, transverse; peristome pentagonal, anterior, transverse; bourrelets moderately to strongly developed; phyllodes slightly widened to broad, single pored; buccal pores present; narrow, naked granular zone in interambulacrum 5 adorally.

*Genera*.—*Clypeolampas*, *Vologesia*.

*Range*.—Cretaceous (Cenomanian-Maestrichtian).

*Comparison with other families*.—The Clypeolampadidae are distinguished from Echinolampadidae by their petals, which have broad poriferous zones of equal length with strongly conjugated pores, whereas in the Echinolampadidae the poriferous zones are narrow, of unequal length in the same petal, and not strongly conjugated.

#### Genus CLYPEOLAMPAS Pomel

*Clypeolampas* Pomel, 1869. Rev. échinodermes, p. 25. Type species by monotypy,

*Clypeaster leskei* Goldfuss, 1829 (= *Galerites ovatus* Lamarck, 1816).

Synonym: *Phylloclypeus* De Loriol.

#### GENERIC DESCRIPTION

Large, elongate, highly inflated, flat adorally, apical system monobasal, anterior; petals broad, open, long, unequal, outer pore of petaloid pores very elongated transversely, slitlike, joined to inner pore by narrow, deep conjugation groove, single pores in ambulacral plates beyond petals; periproct inframarginal, transverse; peristome anterior, pentagonal; bourrelets very prominent, projecting into peristome; phyllodes very broad, single pored, crowded; buccal pores present; two types of tubercles: small scrobiculate, crenulate, perforate tubercles on both adapical and adoral surface except in medial region of interambulacrum 5 adorally; large nonscrobiculate, noncrenulate, nonperforate tubercles on adapical surface and in medial region in interambulacrum 5 adorally.

*Comparison with other genera*.—*Clypeolampas* is most similar to *Vologesia*, but differs in having large tubercles on its adapical surface and a more developed floscelle. It looks very similar, on first impres-



sion, to *Echinolampas* but differs in having much wider poriferous zones of equal length, with deeply conjugated pores.

*Remarks.*—There has been some controversy over whether or not the apical system in *Clypeolampas* was tetrabasal or monobasal. Cotteau (1887, pl. 20, fig. 7) showed a tetrabasal system in his *C. lesteli*. However, the apical system in the type species of the genus, *C. ovatus*, is definitely monobasal as shown in my plate 35, figure 2. I did not see Cotteau's specimen of his *C. lesteli*, but suspect that is probably monobasal also, although it is possible that this character may be variable in this genus.

*Range and distribution.*—Upper Cretaceous (Campanian to Maastrichtian) of Europe and India.

#### DESCRIPTION OF TYPE SPECIES

##### CLYPEOLAMPAS OVATUS (Lamarck)

Plate 35, figures 1-4; text figure 160

*Galerites ovatus* Lamarck, 1816. Animaux sans vertèbres, vol. 3, p. 22.

*Clypeaster leskei* Goldfuss, 1829. Petrefacta Germaniae, p. 132, pl. 42, fig. 1.

*Material.*—Two specimens studied in the École National Supérieure des Mines, three in the Muséum National d'Histoire Naturelle, Paris, one borrowed from General Collignon, and one in the U. S. National Museum.

*Shape.*—Very large, elongate, slightly pointed posterior margin, highly inflated adapically with greatest height at apical system; adorally flat with sharp margin.

*Apical system.*—Anterior, large, monobasal (pl. 35, fig. 2) with inflated madreporite.

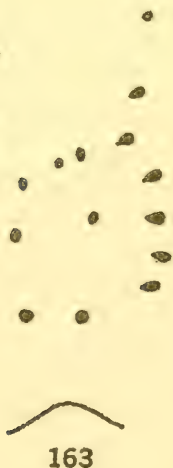
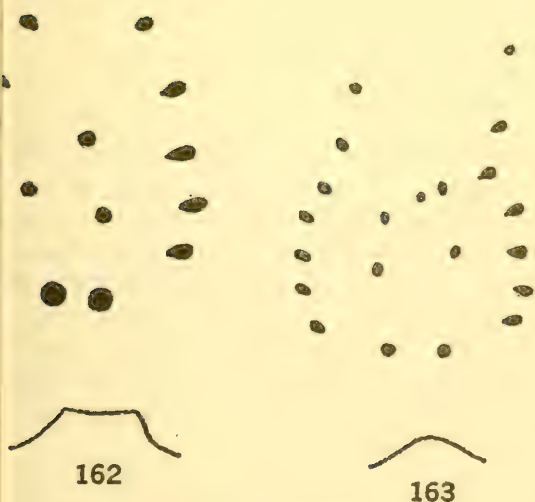
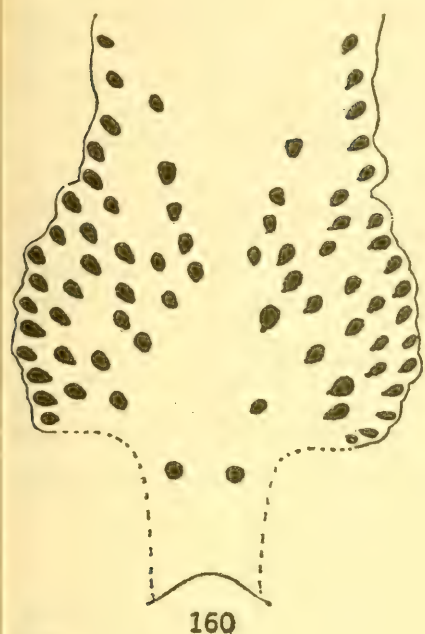
*Ambulacra.*—Petals broad, open, flush, extending to margin, posterior petals longer than others; at extremities interporiferous zones twice width of poriferous zones; outer pore of petaloid pore pair greatly elongated transversely, slitlike, joined to inner pore by deep narrow conjugation pore.

*Periproct.*—Inframarginal, large, transverse, flush with test.

*Peristome.*—Anterior, large, pentagonal, transverse.

*Floscelle.*—Bourrelets very prominent, jutting out over peristome; phyllodes (text fig. 160) large, broad, single pored with many pores, approximately 15 in each outer series of half area, 20 in each inner area, not arranged in series; total of 70 pores in each phyllode; buccal pores present.

*Tuberculation.*—Two types of tubercles: small scrobiculate, crenu-



FIGS. 160-164.—160, *Clypeolampas ovatus* (Lamarck): Phyllode of ambulacrum III of specimen in collection of General Collignon, from the Upper Cretaceous (Maestrichtian), Buzan, France,  $\times 6$ . 161, *Vologesia ovum* (Gratteloup): Phyllode of ambulacrum V of specimen in the De Loriol Collection, Muséum d'Histoire Naturelle, Genève, Switzerland, from the Upper Cretaceous (Senonian) at Bussac de Birac,  $\times 5$ . 162, *Pliolampas gauthieri* (Cotteau): Phyllode of ambulacrum I of lectotype in Lambert Collection, Sorbonne, Paris, from the Miocene (Langhian) and St. Restitut, Drome, France,  $\times 15$ . 163, *Pliolampas pioti* Gauthier: Phyllode of ambulacrum II of specimen in De Loriol Collection, Muséum d'Histoire Naturelle, Genève, Switzerland, from the Miocene, Mont Genéfeh,  $\times 15$ . 164, *Pliolampas vassalli* (Wright): Phyllode of ambulacrum I of specimen ME. 4694 in the British Museum (Natural History), from the Miocene of Malta,  $\times 15$ .

late, perforate tubercles on both adapical and adoral surface except in medial region of interambulacrum 5 adorally; large nonscrobiculate, noncrenulate, nonperforate tubercles on adapical surface and in medial region in interambulacrum 5 adorally.

*Occurrence*.—Upper Cretaceous (Maestrichtian) of France.

*Location of type specimen*.—Not known.

*Remarks*.—Lambert and Thiéry (1921, p. 374) and others have considered Lamarck's *Galerites ovatus* as a nomen nudum and used Goldfuss's *Clypeus leskei* instead. However, Lamarck includes a description of his species, and it cannot be considered a nomen nudum.

#### Synonym of CLYPEOLAMPAS

*Phylloclypeus* De Loriol, 1880. Mém. Soc. Phys. Hist. Nat. Genève, vol. 27, p. 79. Type species by original designation, *Galerites ovatus* Lamarck, 1816.

*Remarks*.—*Phylloclypeus* De Loriol is a junior objective synonym having the same type species as *Clypeolampas*.

#### Genus VOLOGESIA Cotteau and Gauthier

*Vologesia* Cotteau and Gauthier, 1895. Mission en Perse par J. de Morgan, Paléontologie, p. 65. Type species by monotypy, *Vologesia tataosi* Cotteau and Gauthier (op cit., p. 66).

Synonyms: *Hungaresia* Szorenyi; *Pseudovulechinus* Szorenyi.

#### GENERIC DESCRIPTION

Medium to large, inflated, smooth marginal outline, often with greatest width anterior to center, adorally flattened; apical system tetrabasal; petals broad, open, unequal, posterior petals longer than others, outer pore greatly elongated transversely, joined to inner pore by narrow conjugation groove; ambulacral plates beyond petals single pored; periproct inframarginal, transverse; peristome anterior, wider than high, pentagonal; bourrelets well developed, phyllodes broadened, single pored, with many pores; buccal pores present; no large tubercles adapically, tubercles slightly larger adorally, with narrow naked zone in middle of interambulacrum 5.

*Comparison with other genera*.—*Vologesia* is very similar to *Clypeolampas*. Both genera have a large test, strikingly similar petals with narrow, slitlike outer pores in the poriferous zones, inframarginal transverse periproct, and an inflated adapical surface and flattened adoral. *Vologesia* differs in having no large tubercles adapically and in having a less developed floscelle with less inflated bourrelets, and narrower, less crowded phyllodes.

*Remarks.*—I was unable to find any specimens of the type species of this genus but studied seven species of *Vologesia ovum* (Gratelloup), a species that appears to be congeneric with it. I include a photograph (pl. 35, fig. 5) of one of these specimens and a text figure of one of its phyllodes (text fig. 161). The apical system is tetrabasal in this species.

*Range and distribution.*—Upper Cretaceous (Cenomanian to Maestrichtian) of Europe and Persia.

### Synonym of VOLOGESIA

*Hungaresia* Szorenyi, 1955a. Geol. Hung., ser. Palaeont., vol. 26, p. 76. Type species, *Hungaresia hungarica* Szorenyi by original designation.

### DESCRIPTION OF TYPE SPECIES

#### VOLOGESIA HUNGARICA (Szörényi)

Plate 33, figures 5-7; text figures 183, 184

*Hungaresia hungarica* Szörényi, 1955. Geol. Hung., ser. Palaeont., vol. 26, p. 77, fig. 25, pl. 10, figs. 14-22.

*Material.*—Two specimens, a cast of the holotype, and new photographs were studied.

*Shape.*—Large, 53 mm. long, elongate, with well-rounded anterior, posterior margin, highly inflated adapical surface, flat adoral, sharp margin, steep sides.

*Apical system.*—Anterior, tetrabasal, with large madreporite (text fig. 183), small genital plates 3, 4, 1.

*Ambulacra.*—Petals long, open, narrow, with narrow interporiferous zones, wide poriferous zones with conjugate pores, outer pore very elongated transversely, slitlike.

*Periproct.*—Inframarginal, transverse.

*Peristome.*—Very eccentric anteriorly, transverse, pentagonal, small.

*Floscelle.*—Bourrelets well developed, inflated; phyllodes widened, single pored, with two series of pores in each half-ambulacrum (text fig. 184); buccal pores present.

*Location of type specimen.*—Hungarian Geological Institute, Budapest.

*Occurrence.*—Upper Cretaceous (Senonian), Sumeg, Kovesdomb, Bakony.

*Remarks.*—Szörényi states that this species has a monobasal apical system, but the system is definitely tetrabasal (text fig. 183). Her species is almost indistinguishable from *Vologesia ovum* (Gratte-



loup), having the same shape, petal arrangement with slitlike outer pore, tetrabasal apical system, inframarginal transverse periproct, and strikingly similar phyllodes. For this reason *Hungaresia* is herein considered a synonym of *Vologesia*.

#### Synonym of *VOLOGESIA*

*Pseudovulechinus* Szörényi, 1955. Geol. Hung., ser. Palaeont., vol. 26, p. 79.

Type species by original designation, *Pseudovulechinus rotundatus* Szörényi.

*Remarks.*—I have studied one specimen of the type species and suspect that it is an immature specimen of *Vologesia hungarica* Szörényi. This specimen and all the specimens studied by Szörényi are small, and they came from the same locality as the specimens of *V. hungarica*. The specimens referred to *Pseudovulechinus rotundatus* look exactly like what a small specimen of *V. hungarica* would be expected to look like, having a similar high test, petal arrangement, inframarginal periproct, and single-pored phyllodes. Szörényi was not able to discern the apical system on her specimens, but on the specimen sent to me it is definitely tetrabasal.

#### PLIOLAMPADIDAE Kier, new family

Medium to large, elongate, moderately inflated; apical system monobasal, three or four genital pores; periproct inframarginal, usually longitudinal; peristome anterior, usually higher than wide; petals narrow or broad, open or closed, outer pore greatly elongated transversely, strongly conjugate; poriferous zones of same petal of same length; single pore in all ambulacral plates beyond petals; bourrelets well developed, few or many pores; buccal pores present; adoral tubercles slightly larger than adapical, usually no naked, granular zone in interambulacrum 5.

*Genera.*—*Pliolampas*, *Termieria*, *Zuffardia*, *Kephrenia*, *Santee-lampas*, *Neocatopygus*, *Ilarionia*, *Gitolampas*, *Daradaster*, *Eurhodia*, *Studeria*, *Pseudopygaulus*.

*Range.*—Cretaceous (Senonian) to Recent.

*Comparison with other genera.*—The Pliolampadidae are not very homogeneous and may not represent a natural or phylogenetic grouping. They are distinguished from the Echinolampadidae by their lack of a narrow, naked, granular zone in interambulacrum 5 (except in *Ilarionia* and some species of *Gitolampas*), wider outer poriferous zones, and poriferous zones of equal length in the same petal. They differ from the Faujasidae in not having large pointed bourrelets and very broad phyllodes.

Genus *PLIOLAMPAS* Pomel

*Pliolampas* Pomel, 1888. Bull. Soc. Géol. France, ser. 3, vol. 16, p. 446. Type species by monotypy (Pomel, 1883, p. 63, pro *Plesiolampas* Pomel non Duncan and Sladen, 1882), *Echinolampas gauthieri* Cotteau.

Synonyms: *Breynella* Gregory; *Milletia* Duncan.

## GENERIC DESCRIPTION

Medium size, elongate, moderately inflated; apical system monobasal with three or four genital pores, pore may be absent in left anterior genital; petals well developed, open, broad, equal, with broad poriferous zones, conjugate pores, ambulacral plates beyond petals single pored; periproct inframarginal; peristome anterior, higher than wide, pentagonal; bourrelets well developed; phyllodes broad, with large single pores, few in inner series; tubercles slightly larger adorally, no naked granular zone adorally in interambulacrum 5.

*Comparison with other genera.*—*Pliolampas* is distinguished from *Termieria* in having a pentagonal peristome, more crowded phyllodes, and a longer petal III. These differences may only reflect the immaturity of all the specimens known of the type species of *Termieria*, and the two genera may be synonymous. *Pliolampas* differs from *Studeria* in having an inframarginal periproct and less developed bourrelets.

*Remarks.*—There has been considerable confusion and controversy over the number of genital pores in this and related genera. According to Lambert (1913, p. 131) there are only three genital pores in the type specimen of the type species of this genus, *Pliolampas gauthieri*. I have studied this specimen and am uncertain whether there are three or four. The apical area is not well preserved. However, in *Pliolampas pioti* Gauthier there are three or four genital pores. Of the seven specimens of this species in the De Loriol Collection at Geneva, five of them have the apical system preserved. In all five of these there are only three genital pores, no pore being in the left anterior genital (pl. 36, fig. 5). Both Gauthier (*in* Fourtau, 1899, p. 713) and Fourtau (1920, p. 62) report specimens of this species with three or four genital pores. Mortensen (1948, p. 249) admits that "it seems thus incontestable that in this species the number of the genital pores is either four or three." Regardless of this, Mortensen suggests that species with four genital pores should not be placed in *Pliolampas*, but should form a genus of their own. Such an action is unreasonable, as *Pliolampas pioti* with both three and four genital pores would have to be referred to two genera. There

is no question that *Pliolampas pioti* is congeneric with *Pliolampas gauthieri*. Both species have similar shape, broad, equal petals with broad poriferous zones, longitudinal pentagonal peristomes, and strikingly similar phyllodes, broad, with five to six pores in the outer series, one or two in the inner in each half-ambulacrum. As *P. pioti* has never been well figured, I include photographs on plate 36, figures 4-7, and a drawing of a phyllode in text figure 163.

Mortensen (1948, p. 249) states that all species similar to *Pliolampas* having four genital pores should be referred to *Breynella* Gregory; restricting the three-pored species to *Pliolampas*. However, the type species of *Breynella*, *Pliolampas vassalli* (Wright), has only three genital pores. *B. vassalli* is very similar to *P. pioti*, and *Breynella* is considered, herein, a synonym of *Pliolampas*.

Lambert and Thiéry (1921, p. 371) state that a granular sternal zone is a character of *Pliolampas*. However, this zone is not developed in the lectotype of the type species.

*Range and distribution.*—Eocene to Pliocene of the circum-Mediterranean countries and the Malay Archipelago.

#### DESCRIPTION OF TYPE SPECIES

##### PLIOLAMPAS GAUTHIERI (Cotteau)

Plate 36, figures 1-3; text figure 162

*Echinolampas gauthieri* Cotteau, 1880 (reference not seen).

*Material.*—There are two specimens of this species in the Lambert Collection. One of these, the lectotype, was figured by Cotteau in his original description and designated as "type" by Lambert (1913, p. 131). The other specimen is from the same locality but was not figured.

*Shape.*—Medium size, elongate, with pointed posterior margin, slightly inflated with greatest height anterior at apical system, depressed posteriorly; adorally depressed around peristome.

*Apical system.*—Anterior, monobasal, genital pores small, number of pores not certain.

*Ambulacra.*—Petals, similar, broad, open, interporiferous zones narrow; poriferous zones very wide, widening distally, pores deeply conjugate.

*Periproct.*—Inframarginal, transverse.

*Peristome.*—Anterior, longitudinal (higher than wide), pentagonal, depressed.

*Floscelle.*—Bourrelets well developed, inflated; phyllodes broad,

with large single pores (text fig. 162) in two series in each half-ambulacrum: five or six pores in each outer series, one or two in each inner; buccal pores present.

*Tuberculation*.—Adorally, tubercles slightly larger than adapically; no naked medial zone in interambulacrum 5.

*Occurrence*.—Miocene (Langhian), St. Restitut, Drôme, France.

*Location of type specimens*.—Lectotype and figured paratype in Lambert Collection, Sorbonne, Paris.

### Synonym of *PLIOLAMPAS*

*Breynella* Gregory 1891. Trans. Roy. Soc. Edinburgh, vol. 36, pt. 3, No. 22, p. 600. Type species *Pygorhynchus vassalli* Wright, by subsequent designation, Cooke (1942, p. 38).

### DESCRIPTION OF TYPE SPECIES

#### *PLIOLAMPAS VASSALLI* (Wright)

Plate 37, figures 1-4; text figure 164

*Pygorhynchus vassalli* T. Wright, 1855. Ann. Mag. Nat. Hist., ser. 2, vol. 15, pp. 271-272.

*Material*.—I have studied the lectotype (British Museum No. E. 1581) designated by Gregory (1891, p. 602), and one other well-preserved specimen in the same museum.

*Shape*.—Small to medium size, elongate, greatest width posterior to center, adapical surface flat, margins vertical, peristome depressed.

*Apical system*.—Anterior, compact (pl. 37, fig. 2), with three large genital pores, genital 3 not pierced; ocular plates small.

*Ambulacra*.—Petals broad, with wide poriferous zones, narrow interporiferous; pores strongly conjugate, outer pore obliquely elongated, inner pore round; petal III widely open, other petals closing slightly distally; petals V and I longer than others.

*Periproct*.—Marginal to slightly inframarginal, longitudinal.

*Peristome*.—Anterior, higher than wide; pentagonal.

*Floscelle*.—Bourrelets well developed; phyllodes single pored (text fig. 164), with pores arranged in two series in each half-ambulacrum, approximately six pores in each outer series, two in each inner; buccal pores present.

*Ornamentation*.—Adorally, tubercles slightly larger than adapically; no naked, pitted zone in interambulacrum 5.

*Occurrence*.—Miocene (Globigerina limestone) of Malta.

*Location of type specimen*.—British Museum (Natural History).



*Remarks.*—*Breynella* is herein considered a junior subjective synonym of *Pliolampas*. Its type species is very similar to the type species of *Pliolampas*. Both are of similar shape and size with equal, open, and broad petals, with broad poriferous zones, and a longitudinal peristome. In both species the floscelle is well developed, with phyllodes with five or six single pores in each outer series and one or two in each inner.

Lambert and Thiéry (1921, p. 366) considered *Breynella* as a synonym of *Echinanthus* Breynius, but referred all the species that Gregory included in his original description of the genus to *Pliolampas*. Later, they (1924, p. 397) placed *Breynella* as a synonym of *Gitolampas*. *P. vassalli* differs from *Gitolampas* in having broader petals, with wider poriferous, narrower interporiferous zones, and higher than wide peristome. Mortensen (1948, pp. 247, 249) provisionally refers *Breynella* to *Pliolampas*, but because he mistakenly thought that *Breynella* had four genital pores, he suggests that it may be distinct from *Pliolampas*. Cooke (1942, p. 38) considered *Breynella* a synonym of *Echinolampas*, but *Breynella* has much broader equal poriferous zones with the outer pore greatly elongated and strongly conjugate, a longitudinal periproct, and a higher than wide peristome.

#### Synonym of PLIOLAMPAS

##### Genus MILLETIA Duncan

*Milletia* Duncan, 1891. Journ. Linnean Soc. (Zool.), vol. 23, p. 191. Type species by original designation, *Echinolampas elegantulus* Cotteau, 1883. Bull. Soc. Zool. France, vol. 8, pp. 458-460, pl. 15, figs. 6-8. Millet (1854, p. 178; 1865, p. 611) has been considered the author of this species. However, in both these references the name is a nomen nudum with no description, only locality data.

*Remarks.*—I was unable to find any specimens of the type species in Europe. Cotteau (1883, p. 460) states that all the specimens are in the collection of M. l'Abbé Bardin.

Lambert and Thiéry (1921, p. 371) and Mortensen (1948, p. 247) consider *Milletia* a synonym of *Pliolampas*. Its type species is similar to the type species of *Pliolampas* in shape, with a pointed posterior margin, in having broad, equal petals with broad poriferous zones, and in having a longitudinal peristome. It has only three genital pores, a feature common in *Pliolampas*. Cotteau (1883, pl. 15, fig. 8) shows double pores in the phyllodes of *P. elegantulus*. This is certainly a mistake on the part of the artist, as the phyllodes are no

doubt single pored. Cotteau's artist almost invariably showed double pores in the phyllodes whether they were double or single.

*Occurrence*.—Miocene, Chavagnes, Martigné, Doué (Maine et Loire), France.

#### Genus *TERMIERIA* Lambert

*Termieria* Lambert, 1931. Mém. Soc. Géol. France, vol. 7, pp. 30-31. Type species by original designation, *Termieria henrici* Lambert.

#### GENERIC DESCRIPTION

Small, elongate, apical system monobasal; petals broad, unequal, petal III short, pores conjugate; ambulacral plates beyond petals single pored; periproct inframarginal, round; peristome anterior, round; bourrelets and phyllodes slightly developed, phyllodes single pored; buccal pores present.

*Comparison with other genera*.—Lambert placed this genus in the archiacids presumably because of the short petal III. However, this genus is not similar to *Archiacia*. Its shape, petal arrangement, apical system, and phyllodes are completely different. It is most similar to *Phiolampas*, but differs in having a round peristome, narrower phyllodes with fewer pores, and a shorter petal III.

*Remarks*.—It is possible that the only two specimens known of the type species of this genus are immature, and that some of the characters considered to be generic would not occur in mature specimens. Petal III in the lectotype is very short relative to the other petals. In a larger specimen, it would not be so short in proportion to the other petals. Only the difference in the number of pore pairs would remain constant. In the lectotype, there are seven more pore pairs in petals II and IV than in petal III (16 in petals II and IV, 9 in petal III). However, in a larger specimen, although the difference in the number of pore pairs would remain the same (Kier, 1957, p. 851), the proportional difference between the number of pore pairs and, therefore, between the length of the petals, would change. For example, if there were 32 pore pairs in petals II and IV, there would be 25 in petal III, and it would, therefore, be much longer relative to the other petals than it would be in a smaller specimen. The lack of crowding of the phyllodal pores and the small number of sphaeridia in the type specimens may be further evidence that these specimens are immature. Larger specimens, if they occurred, may have had crowded phyllodes and many more sphaeridia. In a growth series in *Echinolampas fraasi* De Loriol (Kier, 1957, p. 851), specimens of

approximately the same size as the specimens of *Termieria henrici* had only slightly crowded phyllodes with very few sphaeridia, whereas in the larger specimens the pores in the phyllodes were very crowded and the sphaeridia very numerous.

*Range and distribution.*—Upper Cretaceous (Maestrichtian) of Morocco. Mortensen (1948, p. 329 and explanation to text fig. 308) refers Duncan and Sladen's *Echinanthus enormis* from the Paleocene of India to *Termieria*. It only resembles *T. henrici* in its short petal III, but in all other characters is quite distinct. The petals in *E. enormis* are longer, narrower, with narrower poriferous zones; the phyllodes are much more developed, with two series of pores in each half-ambulacrum, bourrelets strongly developed, and the test higher. This Indian species seems distinct from any other genus, but as I have seen no specimens of this species, I hesitate to erect a new genus for it.

#### DESCRIPTION OF TYPE SPECIES

##### **TERMIERIA HENRICI** Lambert

Plate 37, figures 5-7; text figure 165

*Termieria henrici* Lambert, 1931. Mém. Soc. Géol. France, vol. 7, p. 31, pl. 1, figs. 31-35.

*Material.*—I have studied the only two specimens, syntypes, known of this species. I designate as lectotype the specimen figured by Lambert (1931) on his plate 1, figures 31-34. This specimen is well preserved adapically and shows the petals clearly. The other specimen, a figured paratype (Lambert, op. cit., pl. 1, fig. 35) is poorly preserved adapically but shows clearly the peristomal region. Apparently no other specimens are known of this species.

*Shape.*—Small, lectotype 14.3 mm. long, elongate, with greatest width posterior to center, low posteriorly, inflated anteriorly, with greatest height near anterior margin; adoral surface flattened, with peristome slightly depressed; posterior margin pointed.

*Apical system.*—Anterior, monobasal.

*Ambulacra.*—Petals broad, with tendency to close distally, of unequal length; posterior petals I and V extending slightly more than one-half distance from apical system to posterior margin, 21 pore pairs in each poriferous zone in lectotype; petals II and IV almost transverse, shorter than posterior petals, with 16 pore pairs in each poriferous zone; petal III very short, less than one-half length of petals II and IV, with 9 pore pairs in each poriferous zone; both

interporiferous and poriferous zones wide, with interporiferous zone slightly wider; pores conjugate, outer pore elongated transversely in all petals but less in petal II than in other petals.

*Peristome*.—Anterior, round, large.

*Periproct*.—Inframarginal, round.

*Floscelle*.—Bourrelets present but slightly developed, no inflated; phyllodes (text fig. 165) slightly developed, single pored, with only slight crowding of the pores near the peristome. Three large pits, presumably for sphaeridia, in each ambulacrum behind the buccal pores, with regular arrangement, first pit half-moon-shaped followed by two round pits.

*Occurrence*.—Upper Cretaceous (Maestrichtian–Danian of Douvillé) from Bekrit, Morocco.

*Location of type specimens*.—Sorbonne (Lambert Collection) Paris, France.

#### Genus ZUFFARDIA Checchia-Rispoli

*Zuffardia* Checchia-Rispoli, 1917. Rend. Roy. Accad. Lincei, ser. 5a, vol. 26, p. 492. Type species by original designation, *Pseudocatapygus sanfilippoi* Checchia-Rispoli.

#### GENERIC DESCRIPTION

Medium, oval, highly inflated; apical system monobasal; petals well developed, broad, ambulacral plates beyond petals single pored; periproct marginal, longitudinal; peristome pentagonal, higher than wide; bourrelets well developed, phyllodes single pored; buccal pores present.

*Comparison with other genera*.—*Zuffardia* is similar to *Pliolampas* in having broad petals with broad poriferous zones of equal length, a longitudinal pentagonal peristome, and similar phyllodes. It differs in having a more inflated test, a marginal periproct, and a smoothly rounded posterior margin.

*Range and distribution*.—Upper Cretaceous (Senonian) of Tripoli.

#### DESCRIPTION OF TYPE SPECIES

##### ZUFFARDIA SANFILIPPOI (Checchia-Rispoli)

Plate 37, figures 8–10; text figure 166

*Pseudocatapygus sanfilippoi* Checchia-Rispoli, 1914. Giorn. Sci. Nat. ed Econ., vol. 30, p. 5, pl. I, figs. 8, 8c.

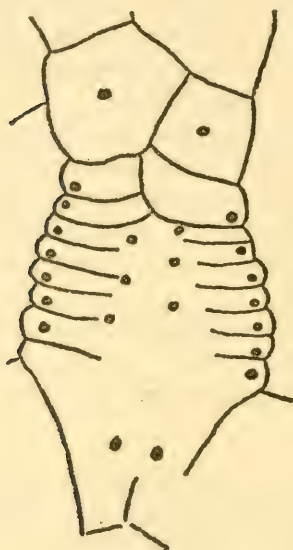
*Material*.—The three type specimens studied.

*Shape*.—Medium size, oval, highly inflated with evenly rounded adapical surface, flat adoral surface around peristome.

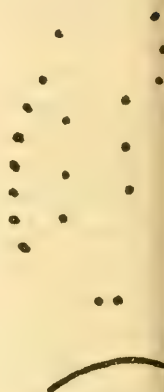




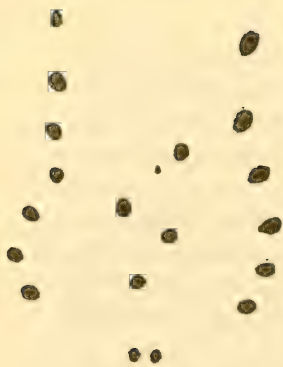
165



166



167



168



169



170

(See legend on opposite page.)

*Apical system*.—Anterior, monobasal, ocular plates very small.

*Ambulacra*.—Petals well developed, broad, closing slightly distally, petals V, I longer than others; poriferous zones very wide, pores conjugate, outer pore slitlike, inner round; interporiferous zones less than twice width of poriferous zones.

*Periproct*.—Marginal, small, longitudinal, pointed adapically.

*Peristome*.—Slightly anterior, pentagonal, higher than wide.

*Phylloscelle*.—Bourrelets well developed, peristome vertically sided. Phyllodes (text fig. 166) single pored, slight broadening near peristome, pores arranged in two series in each half-ambulacrum: five to seven pores in each outer series, three to four in each inner; sphaeridia in two rows along midline of each ambulacrum; buccal pores present.

*Occurrence*.—Upper Cretaceous (Senonian) of Tripoli.

*Location of type specimens*.—Istituto Geologico dell' Università di Palermo.

#### Genus KEPHRENIA Fourtau

*Kephrenia* Fourtau, 1909. Bull. Inst. Égypt., ser. 5, vol. 2, p. 138. Type species by original designation, *Kephrenia lorioli* Fourtau.

#### GENERIC DESCRIPTION

Medium size, elongate, moderately inflated; apical system slightly anterior, monobasal, with four genital pores; petals equal, closed with broad interporiferous, narrow poriferous zones, strongly conjugated pores; ambulacral plates beyond petals single pored; periproct marginal, slightly visible adorally, peristome anterior, pentagonal, higher than wide; bourrelets well developed; phyllodes widened, single pored, two series of pores in each half-ambulacrum; buccal pores present.

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Figs. 165-170.—165, *Termieria henrici* Lambert: Phyllode of ambulacrum III of lectotype in Lambert Collection, Sorbonne, Paris, from the Upper Cretaceous (Maestrichtian), from Bekrit, Morocco,  $\times 21$ . 166, *Zuffardia sanfilippo* (Checchia-Rispoli): Phyllode of ambulacrum IV of holotype in Istituto Geologico dell' Università di Palermo, from the Upper Cretaceous (Senonian) of Tripoli,  $\times 8$ . 167, *Kephrenia lorioli* Fourtau: Phyllode of ambulacrum of holotype in the Geological Museum, Cairo, Egypt, from the Lower Eocene, east of Minia, Egypt,  $\times 15$ . 168, *Santeelampas oviformis* (Conrad): Phyllode of ambulacrum I of USNM 638689, from the Middle Eocene, Santee limestone, at the Santee-Cooper dam, Berkeley County, S. C.,  $\times 15$ . 169, *Neocatopygus rotundus* Duncan and Sladen: Phyllode of ambulacrum I, from specimen C3152 in the collections of the University of California, from the Paleocene of India,  $\times 15$ . 170, *Ilarionia beggiatoi* (Laube): Phyllode of ambulacrum V of Dames' (1878, pl. 5, fig. 2) figured specimen in the Institut und Museum der Humboldt-Universität zu Berlin, from the Eocene, San Giovanni, Vicentin,  $\times 15$ .

*Comparison with other genera.*—Lambert and Thiéry (1921, p. 371) and Mortensen (1948, p. 247) considered *Kephrenia* a synonym of *Pliolampas*. In *Kephrenia*, however, the petals are closed and have narrow poriferous zones, whereas in *Pliolampas* they are open and have very broad poriferous zones. It differs from *Gitolampas* in having a transverse periproct and a higher than wide peristome.

*Remarks.*—Fourtau, in his description of the genus, states that its periproct is supramarginal, but in the holotype of the type species it is marginal to inframarginal and visible adorally.

*Range and distribution.*—Eocene of Egypt.

#### DESCRIPTION OF TYPE SPECIES

##### **KEPHRENIA LORIOLI** Fourtau

Plate 38, figures 1-6; text figure 167

*Kephrenia lorioli* Fourtau, 1909. Bull. Inst. Égypt., ser. 5, vol. 2, p. 139, pl. 9, figs. 1-5.

*Material.*—Holotype and two paratypes studied.

*Shape.*—Small to medium size, low, elongate, posterior margin pointed, anterior margin rounded, greatest width posterior to center, adapical and adoral surface flattened.

*Apical system.*—Slightly anterior, monobasal, four genital pores.

*Ambulacra.*—Petals equal length, broad, closing distally, interporiferous zone twice width of poriferous zone; pore pairs conjugate, outer pore transversely elongate, inner round; poriferous zones tapering distally.

*Periproct.*—Slightly marginal to inframarginal, slightly visible adorally, transverse, slight groove adoral to opening.

*Peristome.*—Anterior, pentagonal, higher than wide, slightly depressed around opening.

*Floscelle.*—Bourrelets well developed; phyllodes single pored (text fig. 167), eight pores in each outer series, three in each inner; buccal pores present.

*Tuberculation.*—Adorally, tubercles slightly larger than adapically; presence or absence of naked medial zone in interambulacrum 5 not clear on specimens studied.

*Occurrence.*—Lower Eocene, east of Minia, Egypt.

*Location of type specimens.*—Geological Museum, Cairo, Egypt.

*Remarks.*—Gorodiski (1951, p. 325) described what he considered to be a variety of this species from the Middle Eocene of Senegal.

## Genus SANTEELAMPAS Cooke

*Santeclampas* Cooke, 1959. Geol. Surv. Prof. Pap. 321, p. 61. Type species by original designation, *Catopygus oviformis* Conrad.

## GENERIC DESCRIPTION

Medium size, elongate, highly inflated, apical system monobasal, very eccentric anteriorly; petals straight, narrow, open, pores conjugate, poriferous zones in same petal of equal length, ambulacral plates beyond petals single pored; periproct marginal, longitudinal; peristome pentagonal higher than wide; bourrelets well developed, phylloides single pored, broad, pores in two series in each half-ambulacrum, few in inner series; no naked zone in interambulacrum 5 adorally.

*Comparison with other genera.*—*Santeclampas* is similar to *Gitolampas* in its peristome, floscelle, and position and shape of its periproct, but differs in having narrower, open petals, and a narrower, more inflated test. It is similar to some species of *Pliolampas* in the shape of its test, but differs in having narrower poriferous zones in its petals and a wider than high peristome. It is distinguished from *Echinolampas* by its petals with poriferous zones of equal length in the same petal, and longitudinal periproct.

*Range and distribution.*—Middle Eocene of eastern United States.

## DESCRIPTION OF TYPE SPECIES

## SANTEELAMPAS OVIFORMIS (Conrad)

Plate 38, figures 7-10; text figure 168

*Catopygus oviformis* Conrad, 1850. Journ. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 2, p. 39, pl. 1, fig. 15.

*Material.*—Holotype and one other specimen studied.

*Shape.*—Medium size, elongate, highly inflated, greatest width and height posterior to center, anterior margin smoothly rounded, posterior pointed when viewed from above, slightly truncated from below, with posterior margin tilted; sides smoothly rounded, adoral surface slightly depressed at peristome.

*Apical system.*—Very eccentric anteriorly, monobasal, four genital pores.

*Ambulacra.*—Petals narrow, long, open, petal III shorter than others, petals V and I longest; poriferous zones narrow, of equal length in same petal, pores conjugate, inner round, outer slightly elongated obliquely; interporiferous zones slightly less than twice



width of poriferous zones; single pores in ambulacral plates beyond petals.

*Periproct*.—Marginal, slightly visible from below, longitudinal, at top of slight groove.

*Peristome*.—Anterior, pentagonal, wider than high.

*Floscelle*.—Bourrelets well developed; phyllodes (text fig. 168) single pored, broad, with four to five pores in each outer series, two in each inner; buccal pores present.

*Tuberculation*.—Adorally, tubercles slightly larger than adapically; no naked zone in interambulacrum 5.

*Occurrence*.—Middle Eocene of South Carolina.

*Location of type specimen*.—Academy of Natural Sciences, Philadelphia, No. 1477.

#### Genus **NEOCATOPYGUS** Duncan and Sladen

*Neocatopygus* Duncan and Sladen, 1882. Pal. Indica, ser. 14, vol. 1, pt. 2, p. 76.

Type species by monotypy. *Neocatopygus rotundus* Duncan and Sladen, 1882.

#### GENERIC DESCRIPTION

Medium size, highly inflated, broad, flat adorally; apical system anterior, monobasal; petals broad, equal in length, closing distally, pores strongly conjugated, oblique to each other, ambulacral plates beyond petals single pored; periproct inframarginal, oval; peristome anterior, pentagonal, wider than high; bourrelets well developed, forming rim around peristome; phyllodes widened, single pored, pores arranged in three series in each half-ambulacrum, buccal pores present; tubercles slightly larger adorally; no naked sternal region.

*Comparison with other genera*.—*Neocatopygus* is most similar to *Gitolampas*, but is distinguished from it by its broader and more highly inflated test.

*Range and distribution*.—Paleocene of India. Only one species is known.

#### DESCRIPTION OF TYPE SPECIES

#### **NEOCATOPYGUS ROTUNDUS** Duncan and Sladen

Plate 39, figures 1-3; text figure 169

*Neocatopygus rotundus* Duncan and Sladen, 1882. Pal. Indica, ser. 14, vol. 1, pt. 2, pp. 76-78, pl. 16, figs. 1-10.

*Material*.—Three specimens were studied from the Museum of Paleontology, University of California, Berkeley, Calif. The lecto-

type is herein designated to be the specimen figured by Duncan and Sladen (op. cit., pl. 16, figs. 1-7). New photographs of this specimen were sent me by the Indian Geological Survey.

*Shape*.—Medium size, lectotype 34 mm. long, margin rounded anteriorly, pointed posteriorly, broad, highly inflated with greatest height posterior to center, steep sides, flat adoral surface with flush peristome.

*Apical system*.—Anterior, monobasal, four genital pores.

*Ambulacra*.—Petals well developed, broad, closed, slightly inflated, equal length, extending two-thirds distance to margin; interporiferous zones twice width poriferous zones at greatest width; poriferous zones broad, pores strongly conjugate, outer pore elongate, situated oblique to inner pore with inner pore nearer apical system; plates beyond petals single pored.

*Periproct*.—On top of posterior prolongation, small, oval, infra-marginal, slightly overhung by adapical surface.

*Peristome*.—Pentagonal, transverse, anterior, flush with test.

*Floscelle*.—Bourrelets well developed, forming rim around peristome; phyllodes (text fig. 169) widened, single pored, flush with test, with three longitudinal series of pores in each half area, 10 to 12 pores in each outer series, 2 to 4 in the middle, 6 to 8 in each inner series; plate sutures visible around inner pores; buccal pores present.

*Tuberculation*.—Adorally, tubercles slightly larger than adapically; apparently no naked sternal area but region not well preserved on any specimen studied by this author.

*Occurrence*.—Paleocene-Ranikot Series, India.

*Location of type specimen*.—Geological Survey of India, Calcutta, India (personal communication from V. R. Khedker).

*Remarks*.—Duncan and Sladen state that the periproct is supra-marginal, but in the new photographs, and their figures of the lectotype, and in all the other specimens I studied, the periproct is low on the posterior margin and visible from below.

#### Genus ILARIONIA Dames

*Ilarionia* Dames, 1878. Palaeontogr., vol. 25, p. 34. Type species by monotypy, *Echinanthus beggiatoi* Laube, 1868.

#### GENERIC DESCRIPTION

Medium size, elongate, inflated with steep sides, flat adorally; apical system anterior, monobasal, four genital pores; petals broad,

closing distally, narrow poriferous zones, ambulacral plates beyond petals single pored; periproct marginal, longitudinal; peristome anterior, pentagonal, usually with rim around opening; bourrelets vertical, not inflated; phyllodes single pored, narrow, few occluded pores; buccal pores present; adoral tubercles only slightly larger than adapical; very narrow, naked, often pitted medial zone in interambulacrum 5 adorally.

*Comparison with other genera.*—*Ilarionia* is very similar to *Gitolampas*, but differs in having less developed phyllodes and bourrelets. In *Ilarionia* the phyllodes are narrow with very few occluded pores, whereas in *Gitolampas* they are widened with a regular inner series of pores in each half-ambulacrum. Furthermore, in *Ilarionia* there is a narrow naked medial zone in interambulacrum 5 adorally, but none in *Gitolampas*. There is usually a rim surrounding the peristome in *Ilarionia*.

*Ilarionia* is distinguished from *Pliolampas* by its narrower poriferous zones, more closed petals, marginal instead of inframarginal periproct, and less developed bourrelets and phyllodes.

*Remarks.*—Mortensen (1948, p. 255) and Lambert and Thiéry (1921, p. 369) state that there is no floscelle in *Ilarionia*. They were probably misled by Dames' erroneous figure of the peristome of the type species. I have seen specimens of both the type species and *Ilarionia sindensis* Duncan and Sladen, and in both species there are vertically sided bourrelets and slightly developed phyllodes.

*Range and distribution.*—Eocene of Europe, India, Madagascar.

#### DESCRIPTION OF TYPE SPECIES

#### ILARIONIA BEGGIATOI (Laube)

Plate 39, figures 4-10; text figure 170

*Echinanthus beggiatoi* Laube, 1868. Sitzungsab. Kais. Akad. Wiss., Math.-Naturw., vol. 29, p. 22.

*Material.*—Two specimens studied from Geologisch-Paläontologisches Institut und Museum der Humboldt-Universität zu Berlin. One of the specimens figured by Dames (1878, pl. 5, fig. 2), the other mentioned by him in his description.

*Shape.*—Medium size, largest of two specimens studied 44 mm. long, elongate, anterior margin smoothly rounded, posterior pointed when viewed from above, blunted when viewed from below; sides steep; adoral surface flat, peristome almost flush with test.

*Apical system*.—Anterior, monobasal, madreporic pores over all central region.

*Ambulacra*.—Petals well developed, very wide, interporiferous zones over twice width poriferous zones, petals closing distally; petals II, III, IV extending almost to margin, petals V, I two-thirds distance to margin, longer than other petals; pores strongly conjugate, inner pore round, outer slightly elongate transversely, joined by deep conjugation groove.

*Periproct*.—Marginal, flush with test, higher than wide.

*Peristome*.—Regular, anterior pentagonal, flush with test, with high wall-like rim surrounding opening.

*Floscelle*.—Bourrelets well developed, vertical sided. Phyllodes (text fig. 170) slightly developed with only slight increase in width of ambulacra near peristome, and slight crowding of pores; approximately three pores occluded in each phyllode; buccal pores present.

*Tuberculation*.—Adorally tubercles only slightly larger than adapically; naked, finely pitted medial area adorally in interambulacrum 5.

*Occurrence of type species*.—Eocene, San Giovanni, Vicentin.

*Location of type specimen*.—Not known.

*Remarks*.—Dames' (1878, pl. 5, fig. 2d) figure of the peristome is diagrammatic and in part erroneous. I was able to study Dames' figured specimen and include an enlarged photograph (pl. 39, fig. 7) of its peristome. The two large tubercles that Dames shows in each ambulacrum at the peristome are not present, and the peristome is deep, with well-developed bourrelets, not shallow and without bourrelets as stated by Dames.

#### Genus GITOLAMPAS Gauthier

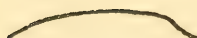
*Gitolampas* Gauthier, 1889a. Éch. foss., Tunisie, pp. 98-99. Type species by monotypy, *Pliolampas tunetana* Gauthier.

Synonyms: *Bothriolampas* Gauthier; *Echanthus* Cooke; *Gitolampopsis* Checchia-Rispoli.

#### GENERIC DESCRIPTION

Medium size, elongate, often with pointed posterior extremity, greatest width posterior to center, rounded margin; apical system monobasal, anterior, four genital pores; petals well developed, broad, closing distally, with broad interporiferous zones, poriferous zones of same petal of same length, pores conjugate, outer pore elongate but not slitlike, ambulacral plates beyond petals single pored; periproct marginal, slightly visible from above or below, longitudinal;

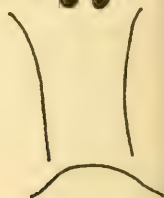
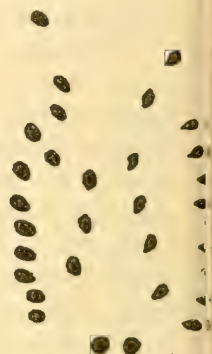




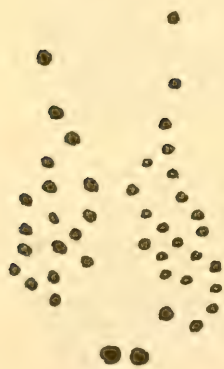
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(See legend on opposite page.)

peristome transverse, anterior, large, subpentagonal; bourrelets well developed, vertical walled; phyllodes broad, single pored, with two or sometimes three series of pores in each half-ambulacrum; buccal pores present.

*Comparison with other genera.*—Some species of *Gitolampas* are very similar to species of *Echinolampas*, but can always be distinguished by their longitudinal periproct, and poriferous zones of equal length in the same petal. This genus is distinguished from *Kephrenia* by its longitudinal periproct and wider than high peristome.

In this genus, the phyllodes usually have two series of pores in each half-ambulacrum, but in a specimen I studied of *G. desmoulini* (Delbos) figured by Cotteau (1888, pl. 162) the phyllodes are very crowded, with the pores in three irregular series (text fig. 174).

*Range and distribution.*—Upper Cretaceous (Senonian) to Miocene of Europe, North Africa, Madagascar, India, and the United States.

*Remarks.*—Included in this genus are many of the species previously referred to *Echinanthus* Breynius (1732). Mortensen (1948, p. 240) and Lambert and Thiéry (1921, p. 366) maintained this genus even though it was pre-Linnean. As discussed on page 226, *Echinanthus* must be attributed to Leske (1778), the first post-Linnean author to use the name. Both *Gitolampas scutella* (Lamarck) and *Gitolampas cuvieri* (Münster) have been considered as the type species of *Echinanthus* Breynius. Both of these species appear to be congeneric with *Gitolampas tunetana*. I have included drawings of a phyllode (text fig. 171), and photographs of the holotype of *G. cuvieri* (pl. 40, figs. 1, 2). Lambert and Thiéry (1921, p. 368) first considered *Gitolampas* a subgenus of *Echinanthus* Breynius, but later (1924, p. 397) separated it. They stated that it differs from *Echinanthus* in having a lower periproct, notched at the margin, and by the

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FIGS. 171-176.—171, *Gitolampas cuvieri* (Münster): Phyllode of ambulacrum II of specimen 763 in the Museum of Comparative Zoology, Harvard, from the Eocene,  $\times 15$ . 172, *Gitolampas georgiensis* (Twitchell): Phyllode of ambulacrum IV of holotype, USNM 165683b, from the Paleocene, Clayton formation on Parker's farm on the Americus road, 5 miles south of Ellaville, Ga.,  $\times 1$ . 173, *Gitolampas issyaviensis* Munier-Chalmas: Phyllode of ambulacrum V of Cotteau's (1888, pls. 154, 155, fig. 1) figured specimen in the École National Supérieure des Mines, Paris, from the Eocene, at Issy, France,  $\times 10$ . 174, *Gitolampas desmoulini* (Delbos): Phyllode of ambulacrum IV of Cotteau's (1888, pl. 162) figured specimen in the École National Supérieure des Mines, Paris, from the Middle Eocene, at Blaye, France,  $\times 8$ . 175, *Gitolampas tunetana* (Gauthier): Phyllode of ambulacrum II of Cotteau's (1890, pl. 245, figs. 6-9; pl. 246, figs. 1-6) in the Lambert Collection, Sorbonne, Paris, from the Lower Eocene, at Mides, Tunisia,  $\times 15$ . 176, *Eurhodia morrisi* Haime: Phyllode of ambulacrum III of specimen C 3632 in the collections of the University of California, from the Paleocene, Ranikot beds, at Petiani, India,  $\times 10$ .

presence of a naked, granular zone adorally. However, many of the species they refer to *Echinanthus* also have a low periproct notched at the margin, and a few of them have the naked granular zone.

Cotteau (1888, Pal. franc., Tert., pl. 154, fig. 6) shows a tetrabasal apical system in *Gitolampas issyaviensis* Munier-Chalmas. I have studied this figured specimen in the Cotteau Collection at the École National Supérieure des Mines in Paris and found a monobasal apical system. Furthermore, in Cotteau's figures of the floscelle of this species and all the other species he figured of *Gitolampas*, he shows double pores in each ambulacral plate of the phyllodes, whereas they are single pored (text fig. 173). Photographs of this specimen are included on plate 42, figures 7-9.

#### DESCRIPTION OF TYPE SPECIES

##### **GITOLAMPAS TUNETANA (Gauthier)**

Plate 42, figures 1-6; text figure 175

*Pliolampas tunetana* Gauthier, 1889. Éch. foss., Tunisie, p. 99, pl. 6, figs. 7-9.

*Material*.—Holotype and two figured specimens studied.

*Shape*.—Small to medium size (holotype, 30 mm. long), elongate, posterior extremity pointed, greatest width posterior to center, margins rounded, adapical surface smoothly convex; adoral surface depressed around peristome.

*Apical system*.—Anterior, monobasal, madreporic pores numerous, occurring over most of apical system, four genital pores.

*Ambulacra*.—Petals long, extending almost to margin, wide, with tendency to close distally; posterior petals longer than others. Interporiferous zones two to three times width of poriferous zones, with greatest width one-third distance from apical system to extremity of petal; poriferous zones narrow, with greatest width at midlength of petal; pores conjugate, outer pore elongated transversely, inner pore less elongated.

*Periproct*.—Marginal to inframarginal, longitudinal, on projected posterior extremity.

*Peristome*.—Anterior, large, subpentagonal.

*Floscelle*.—Bourrelets well developed, vertical walled. Phyllodes (text fig. 175) broadened, single pored, with two series of pores in each half-ambulacrum: approximately 10 in each outer series; 3 to 5 in each inner; buccal pores present.

*Occurrence*.—Upper Cretaceous (Campanian), Djebel Blidji; Djebel Chebika, Midès, Tunisia. Gauthier considered this species to

be Eocene because it was found in a marly limestone rich in the pincers of *Callianassa*. However, as discussed by Fourtau (1909), these beds are not Eocene, but Campanian.

*Location of type specimens.*—The holotype is in the Muséum National d'Histoire Naturelle, Paris, and the specimens figured by Cotteau (1890, pl. 245, figs. 6-9; pl. 246, figs. 1-6) are in the Lambert Collection at the Sorbonne, Paris.

*Remarks.*—Cotteau's figure (1890, pl. 246, fig. 6) of the floscelle is in error in showing double pores in the phyllodes.

#### Synonym of GITOLAMPAS

*Bothriolampas* Gauthier in Fourtau, 1899. Mém. Inst. Égypt., vol. 3, p. 652.

Type species, *Pliolampas tinctana* Gauthier by subsequent designation, Lambert and Thiéry (1921, p. 369).

*Remarks.*—*Bothriolampas* is a junior objective synonym of *Gitolampas*, as both genera have the same type species. Evidently Gauthier forgot that he had already erected a genus for *G. tunetana*.

#### Synonym of GITOLAMPAS

*Echanthus* Cooke, 1942. Journ. Paleont., vol. 16, p. 37. Type species by original designation, *Echinanthus georgiensis* Twitchell.

*Remarks.*—Cooke erected this genus for *Echinanthus* Desor (1858) non Leske (1778). Mortensen (1948, p. 242) misunderstood the basis for Cooke's action and stated that Cooke had considered the type species of his *Echanthus* generically distinct from the species that Mortensen thought to be the type species of *Echinanthus* Desor. Cooke states that *Echanthus* is probably synonymous with *Echinanthus* Desor but erected the new genus because Desor's *Echinanthus* was preoccupied.

*Echanthus* is herein considered a synonym of *Gitolampas*, a genus many workers have considered a subgenus of *Echinanthus* Desor. The type species of the two genera are very similar and certainly congeneric. Both have similar shape, with the greatest width posterior to the center and a pointed posterior extremity; broad petals, with tendency to close distally, periproct longitudinal, marginal or slightly inframarginal, transverse peristome, and similar floscelle. I have included a drawing of the phyllode of *Gitolampas georgiensis* (text fig. 172), and photographs (pl. 40, figs. 3-5) of the holotype.



## Synonym of GITOLAMPAS

Section *Gitolampopsis* Checchia-Rispoli, 1921. Mem. Descr. Carta Geol. d'Italia, vol. 8, pt. 2, p. 18. Type species, *Gitolampas lamberti* Checchia-Rispoli (op. cit.), by subsequent designation, Kier, herein.

*Remarks.*—Checchia-Rispoli proposed this section for his two species *G. lamberti* and *G. zuffardii* from the Senonian of Tripolitania. He distinguished this section from the typical *Gitolampas* by its higher test and more dorsally situated periproct. I have not seen any specimens of the type species, but Checchia-Rispoli's photographs are excellent and permit a comparison of *G. lamberti* with the type species of *Gitolampas*, *G. tunetana*. The periproct in both species is situated in approximately the same position and is not more dorsal in *G. lamberti*. Gauthier's and Cotteau's figures of *G. tunetana* show the periproct in a more ventral position than it really is. It is true that the test is higher in *G. lamberti*, but this character is not of sufficient importance to warrant subgeneric distinction.

## Genus DARADASTER Tessier

*Daradaster* Tessier, 1952. Bull. Dir. Mines, No. 14, p. 295. Type species by monotypy, *Daradaster peroni* Tessier.

## GENERIC DESCRIPTION

Test medium size, elongate, low, apical system very large, monobasal, with genital pores widely separated from each other; petals extremely broad, closed, with poriferous zones of same petal widely separated near apical system; interporiferous zones extremely wide; periproct marginal, peristome anterior, width equal to height; phylloides single pored, greatly widened; bourrelets very strongly developed, extending into peristome, toothlike.

*Comparison with other genera.*—This Eocene genus is similar in shape and petal arrangement to some species of *Gitolampas* but differs in having more strongly developed bourrelets, and a much larger apical system. I was not able to study any specimens of this genus and therefore have included no description of Tessier's (1952, p. 295, pl. 15, figs. 13-15) type species.

## Genus EURHODIA Haime

*Eurhodia* Haime, in d'Archiac and Haime, 1853. Descr. animaux foss. Inde, p. 213. Type species by monotypy, *Eurhodia morrisi* Haime.  
Synonym: *Ravenelia* McCrady.

## GENERIC DESCRIPTION

Medium to large, elongate, low to moderately inflated; adorally flattened, apical system monobasal; petals equal, broad, closing distally, ambulacral plates beyond petals single pored; periproct supra-marginal, transverse or longitudinal; peristome higher than wide; bourrelets strongly developed; phyllodes broad, single pored, with two series of pores in each half-ambulacrum; buccal pores present; tubercles perforate, considerably larger adorally than adapically, except for naked and often pitted adoral interambulacrum 5.

*Comparison with other genera.*—This genus is not very distinctive. Its most distinctive feature is its elongate shape and higher than wide peristome. Mortensen (1948, p. 254) suggested that the genus should be restricted to only those species having a higher than wide peristome, and posterior petals in which the posterior poriferous zones are reduced. This latter feature is known only in the type species and does not seem of generic importance.

Desor's *Cassidulus amygdala* should be referred to *Eurhodia*. It has the elongate test, supramarginal periproct, higher than wide peristome so typical of *Eurhodia*. I studied two specimens of this species in the Cotteau Collection at the École National Supérieure des Mines in Paris.

Cooke (1961, p. 21) transfers Jeannet's (1928, p. 32) *Eurhodia falconensis* to *Cassidulus*. I have seen the holotype in the Naturhistorisches Museum, Basel, Switzerland, and agree with Cooke that it is not a *Eurhodia*. Its test is not sufficiently elongate, and its peristome is wider than high.

*Range and distribution.*—Paleocene-Eocene of India, Europe, North Africa, Madagascar, and North America.

## DESCRIPTION OF TYPE SPECIES

**EURHODIA MORRISI** Haime

Plate 40, figures 6-9; text figure 176

*Eurhodia morrissi* Haime, in d'Archiac and Haime, 1853. Descr. animaux foss. Inde, p. 214.

*Material.*—Ten topotypic specimens were studied from the Museum of Paleontology, University of California, Berkeley, Calif. New photographs were sent from India of the type specimen.

*Shape.*—Medium size, low, very elongate, posterior truncate, greatest width anterior to center, greatest height posterior.

*Apical system.*—Monobasal, anterior.

*Ambulacra*.—Petals well developed, closing distally, wide interporiferous zones almost twice width of poriferous zones, both pores of pore pair elongate transversely, outer pore more elongated than inner, pores conjugate; posterior poriferous zones of petals V and I much narrower than other poriferous zones.

*Periproct*.—Supramarginal, large, transverse, slightly overhung, in slight groove.

*Peristome*.—Much higher than wide, pentagonal, not depressed, anterior.

*Floscelle*.—Bourrelets strongly developed with inflated tips and vertical sides; phyllodes (text fig. 176) broad, single pored, with 10 to 12 pores in each outer series of half-area, 5 to 7 in each inner; buccal pores present.

*Tuberculation*.—Tubercles considerably larger adorally than adapically; deeply scrobiculate with large, high boss located anteriorly in each scrobicule; mamelon very small, perforated; naked median area in interambulacrum 5 and ambulacrum III adorally; few small, round pits in both areas.

*Occurrence*.—Paleocene—Ranikot Series, Petiani, India.

*Location of type specimen*.—Geological Survey of India, Calcutta (personal communication from V. R. Khedker).

*Remarks*.—This species has hitherto been credited to d'Archiac, 1850, p. 248. It is a nomen nudum in this reference and must date from Haime, 1953.

#### Synonym of **EURHODIA**

*Ravenelia* McCrady, 1859. Proc. Elliott Soc. Nat. Hist. Charleston, S. C., vol. 1, p. 283. Type species by subsequent designation, Lambert and Thiéry, 1921, p. 365, *Pygorhynchus rugosa* Ravenel, 1848.

#### DESCRIPTION OF TYPE SPECIES

##### **EURHODIA RUGOSA (Ravenel)**

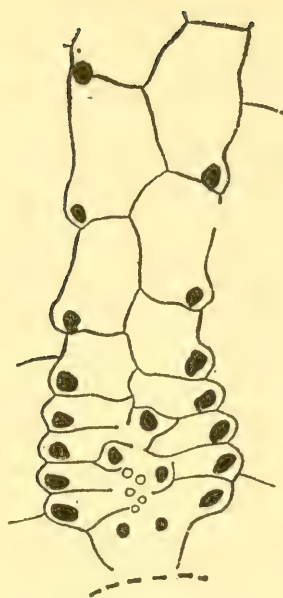
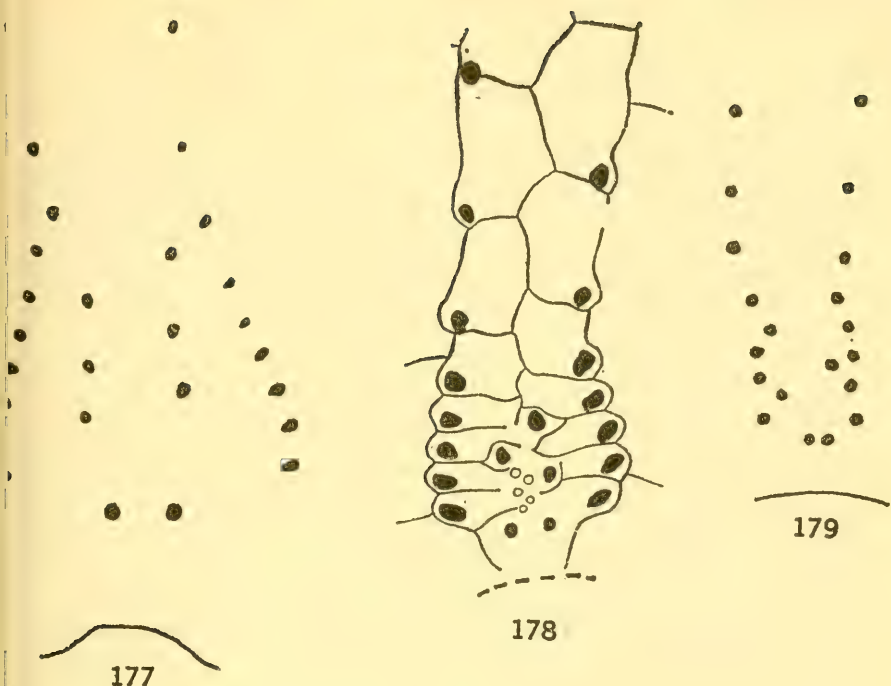
Plate 41, figures 1-5; text figure 177

*Pygorhynchus rugosus* Ravenel, 1848. Echinidae, Recent and fossil, of South Carolina, p. 4, figs. 7, 8.

*Shape*.—Medium size, largest specimen 47 mm. long, very elongate, anterior margin rounded, posterior truncated, sides parallel, adapically low, gently inflated, adorally flattened to slightly depressed.

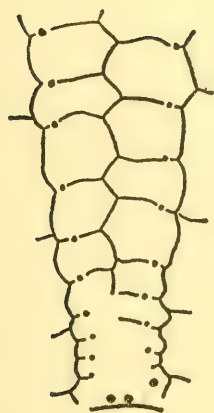
*Apical system*.—Anterior, monobasal.

*Ambulacra*.—Petals broad, with slight tendency to close distally,

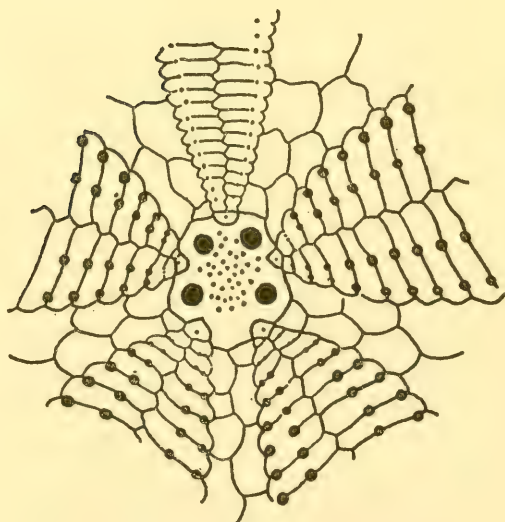


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FIGS. 177-181.—177, *Eurhodia rugosa* (Ravenel): Phyllode of ambulacrum IV of USNM 2300, from the Middle Eocene, Santee limestone, Santee-Cooper Diversion Canal, near Adytown, Berkeley County, S. C.,  $\times 15$ . 178, *Studeria subcarinatus* (Goldfuss): Phyllode of ambulacrum V of specimen in the Lambert Collection, Sorbonne, Paris, from the Oligocene, Bunde, Germany,  $\times 5$ . 179, *Pseudopygaulus trigeri* (Coquand): Phyllode of ambulacrum I of Cotteau's (1887, pl. 126, figs. 6-10) figured specimen in the Ecole National Supérieure des Mines, Paris, from the Upper Eocene, Zouï (Dept. Constantine), near the frontier of Tunisia,  $\times 15$ . 180, 181, *Pseudopygaulus excentricus* (Duncan and Sladen): 180, Phyllode of specimen in the Exeter Museum, Exeter, England, from the Eocene, Khirthar Series of western Sind, India,  $\times 15$ ; 181, apical system of same specimen,  $\times 15$ .



interporiferous zones only slightly wider than poriferous, not tapering distally; poriferous zones wide, tapering distally, with greatest width between one-third and one-half distance from apical system to end of petal; pores conjugate, outer pore more elongated transversely than inner; petals I and V slightly longer than other petals.

*Adoral interambulacra*.—Plates large, alternating; single plate at peristome.

*Periproct*.—Supramarginal, transverse, groove extending from opening to posterior margin, adapical surface overhanging opening.

*Peristome*.—Anterior, pentagonal, higher than wide.

*Floscelle*.—Bourrelets strongly developed (pl. 41, fig. 5), each bourrelet highly inflated, triangular; phyllodes broad (text fig. 177), single pored, pores arranged in two series in each half-ambulacrum: seven to nine in each outer series, three to four in each inner. Buccal pores present; sphaeridia in two rows in median of each phyllode.

*Tuberculation*.—Tubercles on adoral surface much larger than on adapical; deeply scrobiculate, with large high boss located anteriorly in each scrobicule; mamelon very small, perforated. Deep, irregularly shaped pits in adoral interambulacra, many in naked median area in interambulacrum 5, a few in ambulacrum III.

*Occurrence*.—Middle Eocene, Santee limestone of North and South Carolina.

*Location of type specimen*.—Unknown. Cooke (1959, p. 64) suggests that it might be in the Charleston Museum, Charleston, S. C.

*Remarks*.—I agree with Lambert and Thiéry (1921, p. 365), Mortensen (1948, p. 252), and Cooke (1959, p. 63) in considering *Ravenclia* a synonym of *Eurhodia*. The type species of both genera have the same elongate, low shape, with supramarginal transverse periproct, high peristome, and strikingly similar floscelle. They differ only in that *E. morrissi* is more inflated, has wider petals, and has smaller and fewer pits on the adoral surface.

#### Genus *STUDERIA* Duncan

*Studeria* Duncan, 1891. Journ. Linn. Soc. (Zool.), vol. 23, p. 185. Type species by monotypy, *Catopygus elegans* Laube.

Synonyms: *Hypselolampas* Clark; *Phaleropygus* De Loriol; *Tristomanthus* Bittner.

#### GENERIC DESCRIPTION

Small to medium, elongate, smoothly rounded anterior margin, pointed or slightly truncated posterior, adorally depressed around peristome, moderately inflated; apical system anterior, monobasal,

three genital pores, no pores in left anterior genital plate; petals long, straight, extending almost to margin, open, adjacent pore pairs widely spaced, ambulacral plates beyond petals single pored; periproct marginal, longitudinal, slight groove extending adorally; peristome anterior, slightly higher than wide; bourrelets very strongly developed, inflated; phyllodes slightly widened, single pored, with few pores; buccal pores present; tubercles slightly larger adorally, no naked, granular zone in interambulacrum 5.

*Comparison with other genera.*—*Studeria* is very similar to *Pliolampas*, as both genera have open petals, usually three genital pores with no pore in the left anterior genital plate, similar phyllodes, and a higher than wide peristome. *Studeria* differs in having a marginal periproct, and more developed bourrelets. Perhaps these differences are not of sufficient importance to warrant maintenance of *Studeria*.

*Remarks.*—Mortensen (1948, p. 234), along with many earlier workers, considered *Studeria recens* A. Agassiz as the type species of *Studeria*. However, as Duncan mentions only one species, *S. elegans*, in his original description of this genus, *S. elegans* must be the type species by monotypy.

I have been unable to find any specimens of the type species but include below a description of a very similar species, *S. subcarinatus* (Goldfuss).

*Range and distribution.*—Oligocene to Recent of Europe, Egypt, and Australia.

#### Synonyms of *STUDERIA*

*Hypselolampas* H. L. Clark, 1917. Mem. Mus. Comp. Zool., vol. 46, No. 2, p. 104. Type species by original designation, *Studeria recens* A. Agassiz.

*Remarks.*—I have not seen any specimens of the type species, but from a study of Agassiz's figures I can see no characters of sufficient importance to warrant generic distinction for Clark's genus.

*Phaleropygus* De Loriol, 1902. Notes pour servir à l'étude des échinodermes, p. 15. Type species by monotypy, *Phaleropygus oppenheimi* De Loriol.

*Remarks.*—I was unable to find any specimens of this species in the De Loriol Collection in Genève, but from a study of his figures, this species appears to be congeneric with *Studeria*. Both Lambert and Thiéry (1921, p. 372) and Mortensen (1948, p. 372) also considered *Phaleropygus* a synonym of *Studeria*.

Synonym of **STUDERIA**

*Tristomanthus* Bittner, 1892. Sitzungsab. Kais. Akad. Wiss., Math.-Nat. Classe, vol. 101, Bd. 3, p. 355. Type species by subsequent designation, Lambert (1906, p. 41), *Nucleolites subcarinatus* Goldfuss.

## DESCRIPTION OF TYPE SPECIES

**STUDERIA SUBCARINATUS** (Goldfuss)

Plate 41, figures 6-9; text figure 178

*Nucleolites subcarinatus* Goldfuss, 1826. Petrefacta Germaniae, p. 142, pl. 143, fig. 10.

*Material*.—Two specimens studied from the Lambert Collection, Sorbonne, Paris, and four specimens in the U. S. National Museum.

*Shape*.—Medium size, oval, posterior slightly truncated, slight ridge in median suture of interambulacrum 5 on adapical side, greatest width at center, greatest height posterior; peristome deeply depressed.

*Apical system*.—Slightly anterior, monobasal, only three genital pores, no pore in genital 3.

*Ambulacra*.—Petals equal length, open, interporiferous zones same width as poriferous zones; pores conjugate, outer pore slightly elongated transversely, conjugation grooves deep; pore pairs widely spaced; single pores in ambulacral plates beyond petals.

*Periproct*.—Slightly supramarginal, longitudinally elongate, with groove extending from adoral side of opening to posterior margin.

*Peristome*.—Central to slightly anterior, deeply depressed, pentagonal, higher than wide.

*Floscelle*.—Bourrelets very strongly developed; phyllodes widened, single pored (text fig. 178), slightly developed but with large pores; five or six in each outer series, one to two in each inner series; buccal pores present.

*Tuberculation*.—Adorally tubercles only slightly larger than adapically; no naked, granular zone in interambulacrum 5.

*Occurrence*.—Oligocene of Germany.

*Location of type specimen*.—Not known.

*Remarks*.—There is little doubt that *Tristomanthus* is a synonym of *Studeria*. The type species of both genera are very similar, having open petals with deep conjugation grooves, only three pores in the apical system with no pore in the left anterior genital plate, a marginal longitudinal periproct, a peristome higher than wide, deeply depressed, well-developed bourrelets and similar phyllodes.



Genus **PSEUDOPYGAULUS** Coquand

*Pseudopygaulus* Coquand, 1862. Mém. Soc. Emulation de la Provence de Constantine, vol. 2, Marseille, pl. 31 (explanation). Type species by monotypy, *Catopygus trigeri* Coquand.

Synonyms: *Eolampas* Duncan and Sladen; *Ottiliaster* Penecke; *Petalaster* Cotteau.

## GENERIC DESCRIPTION

Small, elongate, inflated; apical system anterior, monobasal; ambulacrum III not petaloid, other ambulacra petaloid with broad petals, usually closed, pores conjugate, ambulacral plates beyond petals single pored; periproct inframarginal, transverse, oval or triangular; peristome slightly anterior, transverse, oval; bourrelets present but not inflated; phyllodes single pored with slight crowding of pores, buccal pores present.

*Comparison with other genera.*—*Pseudopygaulus* is similar to *Termieria* in having broad petals, an oval peristome, a transverse and inframarginal periproct, similar tuberculation, and phyllodes with few pores. It differs in having no petal in ambulacrum III.

*Remarks.*—There has been considerable controversy over the validity of this genus. Coquand did not name the genus in his text, but called the type species *Catopygus trigeri*. However, in the plate explanation he called it *Pseudopygaulus trigeri*. Duncan (1891, p. 200), Lambert (1911b, pp. 181-183), and Lambert and Thiéry (1921, p. 360) considered Coquand's *Pseudopygaulus* a nomen nudum and used Duncan and Sladen's *Eolampas* in its place. Cotteau (1887, pp. 467-469, 1890, pp. 48, 49), Gauthier (1885, pp. 69-71), Pomel (1887, p. 118) and Fourtau (1909, p. 135) preferred *Pseudopygaulus*. Mortensen (1948, p. 328) was uncertain whether or not Coquand's genus was a nomen nudum and stated that "the name *Eolampas* has gradually gained ground, and as no special interest attaches to any of them, and as *Eolampas* is the more easy of the two I think it preferable." However, Coquand's *Pseudopygaulus* is not a nomen nudum, for the name was published and accompanied with an indication, illustrations in this case.

Lambert and Thiéry (1921, pp. 359, 360) refer *Pseudopygaulus* to Gauthier (1885, p. 69) and state that it was founded on entirely different characters than Coquand's *Pseudopygaulus*. They are mistaken, as Peron and Gauthier's text figures of their specimens of *P. trigeri* show a specimen very similar to Coquand's.

*Range and distribution.*—Paleocene-Eocene of France, Austria, Madagascar, North Africa, and India. There are 9 or possibly 10



(if *P. pusillus* Penecke is included) species known in this genus. I have studied the type specimen of *P. buccalis* Peron and Gauthier, and *P. gauthieri* Cotteau, and a figured specimen of *P. trigeri*, all of which are in the Lambert Collection at the Sorbonne. The type specimen of *P. lorioli* Cotteau was seen in the De Loriol Collection at the Muséum d'Histoire Naturelle, Genève, Switzerland, and a specimen of *P. maresi* (Cotteau) in the Cotteau Collection at the École National Supérieure des Mines in Paris. The type specimen of *P. excentricus* and *P. antecursor* (Duncan and Sladen) are in the collections of the Geological Survey of India at Calcutta, and were not seen.

#### DESCRIPTION OF TYPE SPECIES

##### PSEUDOPYGAULUS TRIGERI (Coquand)

Plate 43, figures 5-8; text figure 179

*Catopygus trigeri* Coquand, 1862. Mém. Soc. Emulation de la Provence de Constantine, vol. 2, Marseille, p. 274, pl. 31, figs. 14-16 (labeled *Pseudopygaulus trigeri* on plate explanation).

*Material*.—Four specimens studied in the Cotteau Collection in the École National Supérieure des Mines in Paris, including a figured specimen (Cotteau 1887, pl. 126, figs. 5-10), and one figured specimen (Cotteau, op. cit. pl. 126, figs. 1-5) in the Gauthier Collection which is in the Lambert Collection at the Sorbonne, Paris. All the specimens are silicified, and some of them are very well preserved.

*Shape*.—Small, 20 mm. long, elongate with pointed posterior margin, inflated adapical surface with greatest height anterior at apical system; adorally flattened except for depressed area around peristome.

*Apical system*.—Anterior, monobasal.

*Ambulacra*.—Anterior ambulacrum not petaloid, with two series of pores, each ambulacral plate single pored. Other ambulacra petaloid, broad, closed, petals II and IV slightly shorter than petals I and V; interporiferous and poriferous zones wide, tapering distally. Pores strongly conjugate, outer pore elongated transversely, inner less elongated, joined by deep groove.

*Periproct*.—Inframarginal, triangular, wider than high.

*Peristome*.—Anterior, oval, wider than high.

*Floscelle*.—Bourrelets not inflated; phyllodes not broadened, single pored with slight crowding of pores (text fig. 179), one or two pores occluded in each half-ambulacrum. Buccal pores present.

*Occurrence*.—Upper Eocene, Zouï (Department of Constantine), near frontier of Tunisia. Lambert (1911b), p. 184) refers specimens to this species from Grangeot, near Fabrezan, and near Coustouge, Aube, France.

*Location of type specimen*.—Unknown.

*Remarks*.—Cotteau (1887, p. 473, pl. 126, fig. 4) describes and figures the apical system as tetrabasal. In all the specimens I studied, including the one figured by Cotteau, the apical system was monobasal. Cotteau (op. cit., pl. 126, figs. 3-5) shows pore pairs in ambulacrum III adapically and pore pairs in the phyllodes. This is an error, for all the ambulacral plates in ambulacrum III, and in the ambulacral areas beyond the petals, and in the phyllodes are single pored.

#### Synonym of *PSEUDOPYGAULUS*

*Eolampas* Duncan and Sladen, 1882. Pal. Indica, ser. 14, vol. 1, p. 61. Type species by monotypy, *Eolampas antecursor* Duncan and Sladen.

*Material*.—I have not seen any specimens of the type species. The type specimen is at the Geological Survey of India (personal communication from V. R. Khedker). Pictures of this specimen were very kindly sent to me. I have studied specimens of *P. excentricus* (Duncan and Sladen), a species considered by Duncan and Sladen to be congeneric with their *P. antecursor*. These specimens are at the Exeter Historical Museum, Exeter, England, and in the Muséum National d'Histoire Naturelle, Paris.

*Remarks*.—When Duncan and Sladen erected their genus *Eolampas*, they were not aware of *Pseudopygaulus*, or did not consider it a valid genus. In 1887 they stated that *Pseudopygaulus* and *Eolampas* were synonymous, and all later authors have agreed. The only controversy has been over which name had priority.

Both type species are very similar, having a small test, nonpetaloid ambulacrum III, broad petals, inframarginal and transverse periproct, oval peristome, slightly developed bourrelets, and single-pored phyllodes with slight crowding of the pores. They differ in that the petals in *P. antecursor* and *P. excentricus* have narrower poriferous zones, a character probably not of sufficient significance to warrant maintenance of *Eolampas* as separate from *Pseudopygaulus*. I have included a drawing of the phyllode, and of the apical system (text figs. 180, 181), and photographs (pl. 43, figs. 1-4) of *P. excentricus*.

Synonym of *PSEUDOPYGAULUS*

*Ottiliaster* Penecke, 1885. Sitzungsab. Kais. Akad. Wiss., vol. 90, p. 350. Type species by monotypy, *Ottiliaster pusillus* Penecke.

*Remarks.*—Lambert and Thiéry (1921, p. 359), Collignon (1930, p. 550), and Mortensen (1948, p. 326) considered *Ottiliaster* a synonym of *Pseudopygaulus* or *Eolampas*. I have not been able to locate any specimens of the type species, but from Penecke's figures it appears to be congeneric.

*Location of type specimen.*—Unknown.

Synonym of *PSEUDOPYGAULUS*

*Petalaster* Cotteau, 1885. Bull. Soc. Zool. France, vol. 9, p. 330. Type species by monotypy, *Petalaster maresi* Cotteau.

*Remarks.*—Cotteau (1887, p. 468-469) stated that when he erected his genus *Petalaster* he did not know that Coquand had named a new genus for *Pseudopygaulus trigeri*, a species that Cotteau considered congeneric with his *Petalaster maresi*. He, therefore, placed his *Petalaster* in synonymy under *Pseudopygaulus*. I have seen a specimen of *P. maresi* and agree that it is certainly congeneric with *P. trigeri*. They are so similar that they appear to be almost conspecific. Cotteau (1887, pl. 128, figs. 7, 8) shows double pores in the phyllodes and in ambulacrum III of *P. maresi*. This same error occurs in all his drawings of the other species of *Pseudopygaulus*.

*Location of type specimen.*—I was unable to locate the type specimen but did find one specimen of this species in the Cotteau Collection in the École Nationale Supérieure des Mines in Paris.

## Family APATOPYGIDAE Kier

Medium size, elongate, apical system tetrabasal in young, monobasal in adult; petals moderately developed, ambulacral plates beyond petals single pored; periproct supramarginal; bourrelets slightly developed, phyllodes single pored with two rows of pores in each half-ambulacrum; no buccal pores; "Pyrinid" plates in ambulacra beyond petals.

*Genus.*—*Apatopygus*.

*Range.*—Upper Tertiary to Recent.

*Remarks.*—The Apatopygidae are distinguished from all the other cassiduloid families by their single-pored phyllodes lacking buccal pores, and "Pyrinid" plating in the ambulacra beyond the petals.



**Genus APATOPYGUS** Hawkins

*Apatopygus* Hawkins, 1920b. Geol. Mag., vol. 57, pp. 393-401. Type species by original designation, *Nucleolites recens* M. Edwards.

## GENERIC DESCRIPTION

Medium size, low, apical system tetrabasal in young, monobasal in adults, four genital pores; petals narrow, open, pores conjugate; "Pyrinid" plating in ambulacra beyond petals; periproct supramarginal, in groove extending to posterior margin; peristome, low, not pentagonal; bourrelets slightly developed; phyllodes single pored, not widened, with two series of pores in each half-ambulacrum; no buccal pores; no naked, granular zone in interambulacrum 5 adorally.

*Comparison with other genera.*—*Apatopygus* resembles in general appearance *Nucleolites* having a supramarginal periproct and similarly shaped test, but differs in having single pores in the ambulacral plate beyond the petals, in having a monobasal apical system in the adults, and in having "Pyrinid" plating in the ambulacra beyond the ambitus. Hawkins placed his genus in the Nucleolitidae, but these differences seem of too great significance to permit *Nucleolites* and *Apatopygus* to be included in the same family. *Apatopygus* is so different from any other genus of the Cassiduloidea that it seems advisable to erect a new family for it. I was able to study a specimen of the type species in the Museum of Comparative Zoology, Harvard, and include photographs (pl. 34, figs. 4-7), and a drawing of its phyllodes (text fig. 182). As Mortensen (1922, p. 184), Brighton (1929), and Hawkins have given excellent descriptions of this species, no description is included herein.

## INCERTAE SEDIS

**Genus ASTROPYGAULUS** Checchia-Rispoli

*Astropygaulus* Checchia-Rispoli, 1945. Boll. Ufficio Geol. d'Italia, vol. 68, p. 2. Type species by monotypy, *Astropygaulus trigonopygus* Checchia-Rispoli.

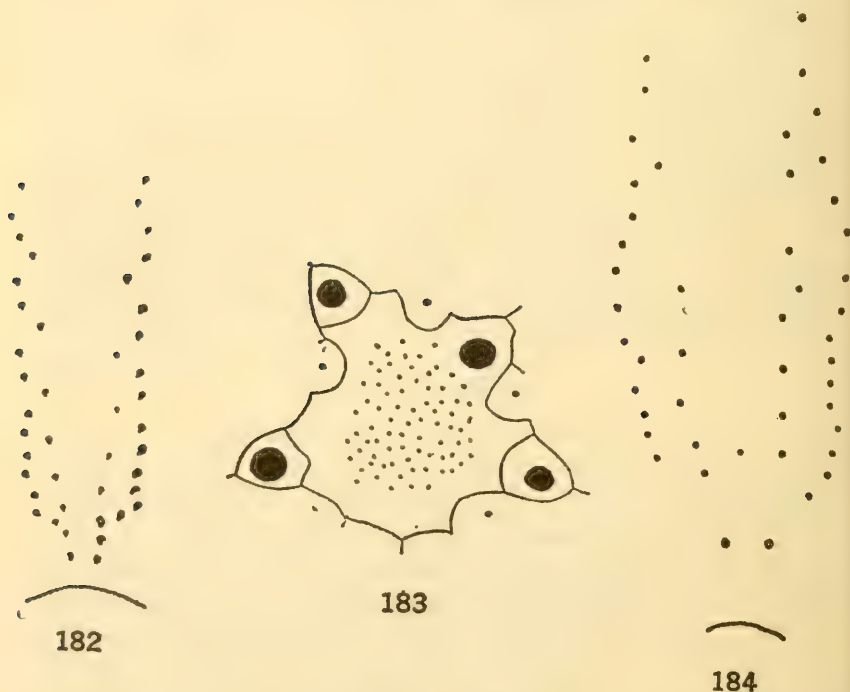
*Remarks.*—This genus is based on a fragment of one specimen, and it is not possible to know all the characters of the type species. The test is low, wide, with wide, closed petals and resembles very much *Pygurus*. The peristome, however, is oblique, and because of this, Checchia-Rispoli considered the genus most similar to *Pygaulus*. An oblique peristome also occurs in *Pygorhynchus*, and this species seems more closely related to that genus. However, not enough is known of this genus to permit definite assignment to any family, and it seems advisable to place it in incertae sedis.



Genus *CENTROPYGUS* Ebray

*Centropygus* Ebray, 1858, Bull. Soc. Géol. France, ser. 2, vol. 15, p. 483. Type species by subsequent monotypy, *Antropygus guetinicus* Ebray, 1859.

*Remarks.*—Because the genus and type species of *Centropygus* have never been adequately described or figured, there is considerable uncertainty as to the value of this genus. Ebray erected this genus because he considered its apical system to be distinctive, having small, separated oculars II and IV. The type species has never been adequately described or figured. In his original generic description, Ebray refers no species to the genus but gives a rather diagrammatic drawing of its apical system. Later, he (1859, p. 759) states in a footnote that the genus has for its type *Anthropygus guetinicus*. According to Lambert and Thiéry (1921, p. 337) the "Anthropygus" is a typographical error for *Centropygus*. Presumably, the apical system figured in his earlier paper is of *Centropygus guetinicus*. This



FIGS. 182-184.—182, *Apatopygus recens* (Milne Edwards): Phyllode of ambulacrum IV of specimen 856 in the Museum of Comparative Zoology, Harvard,  $\times 6$ . 183, 184, *Vologesia hungarica* (Szörényi): Apical system,  $\times 15$ , and phyllode IV,  $\times 10$ , of USNM 131284, from the Upper Cretaceous (Senonian), Sumeg, Kovesdomb, Bakony.

is the only figure known of this species. I was unable to find any specimens of this species in the Paris museums and suspect that there are none. From Ebray's brief description of the genus, it appears to be similar to *Hyboclypus* except for its apical system which differs from *Hyboclypus* in having smaller oculars II and IV. This character alone does not seem to warrant generic distinction for *Centropygus*, but until more is known of the type species it seems advisable to refer this genus to incertae sedis.

In his original description of the genus, Ebray spells it both "*Centropygus*" and "*Centroclypus*." The first subsequent author to discuss these differences in spelling was Lambert (1935, p. 530), and as first reviser, his decision to use "*Centropygus*" should be followed.

#### Genus *CLAVIASTER* d'Orbigny

*Claviaster* d'Orbigny, 1856. Pal. Franc., Crétacé, ser. 1, vol. 6, p. 281. Type species by original designation, *Archiacia cornuta* Agassiz.

*Remarks.*—Four species have been referred to this genus, and in none of the specimens of any of these species is the adoral surface preserved. Nothing is known therefore about the peristome, floscelle, if present, or peripoct. It is not possible to know the affinities of this genus, or whether it is even a cassiduloid. Most authors have considered *Claviaster* a close relative of *Archiacia*. Both genera have a highly inflated test and a nonpetaloid ambulacrum III. However, these two similarities do not seem to be sufficient evidence for considering these genera as close relatives. The petals in *Claviaster* are very different from those of *Archiacia*. There is no way of predicting the character of the adoral surface of *Claviaster*, and it may have been entirely different from that of *Archiacia*. For this reason *Claviaster* is not placed with *Archiacia*, but in incertae sedis.

I have included photographs of the holotype of both *C. cornutus* (pl. 23, fig. 1) and *C. libycus* Gauthier (pl. 23, fig. 2). Both of these specimens are in the Muséum National d'Histoire Naturelle, Paris.

Pomel's (1883, p. 55) *Passalaster* is probably a synonym of *Claviaster*. He based the genus on his species *Claviaster costatus*, this species in turn being based on a specimen that Cotteau had referred to *C. cornutus*. Because Cotteau had said that all the ambulacra were similar, whereas ambulacrum III is different from the others in *C. cornutus*, Pomel made a new species for the specimen, and a new genus for the species. However, Lambert and Thiéry (1921, p. 359) state that Cotteau was mistaken and that

ambulacrum III is different from the others. They therefore consider *Passalaster* a synonym of *Claviaster*.

#### Genus CLYPEANTHUS Cotteau

*Clypeanthus* Cotteau, 1894. Assoc. Franc. Avanc. Sci., Congr. Besancon, vol. 22, p. 354. Type species by monotypy, *Toxaster pentagonalis* Fraas.

*Remarks.*—I was unable to find any specimens of the type species and only species known of this genus. Cotteau's figures do not show many of the important characters of the test such as the apical system, phyllodes, or shape of peristome. Having a reduced petal III and an inframarginal periproct, this genus resembles *Gentilia* and may be synonymous with it, but without seeing any specimens, it seems best to place the genus in incertae sedis.

#### Genus ECHINANTHUS Leske

*Echinanthus* Leske, 1778. Klein's Nat. disp. ech., p. 121. Type species herein designated, *Echinanthus ovatus* Leske (op. cit., p. 127, pl. 20, figs. c, d).

*Remarks.*—There has been considerable controversy over the genus *Echinanthus*. Mortensen (1948, pp. 240-243) credited *Echinanthus* to Breynius (1732), and chose to ignore Leske's (1778) use of the name. As Breynius is pre-Linnean, and Leske was the first post-Linnean author to use *Echinanthus*, the genus must be credited to Leske, and one of the four species he referred to this genus must be considered as its type species. Two of these species, *Echinanthus humilis* and *Echinanthus altus*, can be referred definitely to *Clypeaster*, and a third, *Echinanthus orbiculatus*, to *Pygurus*. Since *Echinanthus* has priority over both of these genera, the selecting of one of these three species as the type species of *Echinanthus* would make *Clypeaster* or *Pygurus* a synonym of *Echinanthus*. Such action would create considerable confusion. The fourth species, *Echinanthus ovatus*, has long been considered the type species of *Echinolampas*. However, it is not clear from Leske's figure that his specimen represents the species which is now considered as *Echinolampas ovatus*. Because of this uncertainty, it seems best to restrict *Echinanthus ovatus* to Leske's specimen (now lost), and designate it as the type species of *Echinanthus*. By this action the genera *Pygurus*, *Clypeaster*, and *Echinolampas* remain valid. Leske's figure of *E. ovatus* is so poor that it is not possible to know most of the generic characters of the species, and because of this the genus *Echinanthus* is referred to incertae sedis.

Most of the species that have been referred by other authors to *Echinanthus* are herein referred to *Gitolampas*.

**Genus JOLYCLYPUS Lambert**

*Jolyclypus* Lambert, 1918. Mém. Soc. Acad. Aube, ser. 3, vol. 55, p. 26. Type species by original designation, *Galeropygus jolyi* Gauthier.

*Remarks.*—I was unable to find any specimens of the type species of this genus. Lambert created this taxa as a subgenus of *Galeropygus* from which it differs in having a more elongate test and higher ambulacral plates. However, the species is based on a few very small specimens which may be immature. I suspect that the age, supposed to be Cenomanian, of this species is incorrect, as it appears to be far too primitive. Until specimens of the type species can be reexamined, it seems preferable to place this genus in incertae sedis.

**Genus LOVENILAMPAS Maury**

*Lovenilampas* Maury, 1934a. Amer. Mus. Nov., No. 744, p. 3. Type species by original designation, *Lovenia baixadoleitensis* Maury.

DESCRIPTION OF TYPE SPECIES

**LOVENILAMPAS BAIXADOLEITENSIS Maury**

Plate 43, figures 9, 10

*Lovenia baixadoleitensis* Maury, 1934b, Bull. Amer. Mus. Nat. Hist., vol. 67, p. 156, pl. 15, fig. 1.

*Remarks.*—I have studied the type specimen in the American Museum of Natural History, New York. It is just a fragment of an external cast of the area around the mouth. Maury did not realize that the specimen was a cast, but considered it to be an internal mold. The "extraordinary coating of cushions covering the inner surface of the plates of the test" Maury describes are in reality only the impressions made by the tubercles. It is not possible to refer this Cretaceous (Turonian) fragment to a genus, but the phyllodes are similar to those found in *Pygorhynchus*.

**Genus OVULECHINUS Lambert**

*Ovulechinus* Lambert, 1920a. Mém. Soc. Acad. Aube, vol. 84, pp. 148, 149. Type species by original designation, *Ovulechinus pilula* Lambert (op. cit., pp. 148, 149, pl. 1, figs. 7-9).

*Remarks.*—This genus is based on one species, represented by two very poorly preserved and probably immature specimens. These



specimens were studied by this author in the Lambert Collection at the Sorbonne, Paris. The specimen figured by Lambert is herein designated the lectotype. Both specimens are badly weathered, with the details of their tests obscured by secondary calcite. The lectotype is 9 mm. long and the paratype 8.5. The test is oval, highly inflated, with rounded adapical surface, and slightly flattened adoral. The structure of the apical system is not clear, but no genital pores are visible. They probably were never present on these specimens, their absence indicating the immaturity of these individuals. Kier (1957, p. 849) found that no genital pores occurred in specimens less than 14 mm. long of *Echinolampas fraasi* De Lorient. There is no indication of petals, their absence again reflecting the immaturity of the individuals. The periproct is inframarginal and transverse, and the peristome is anterior, transverse, with slightly developed bourrelets. No details are visible of the phyllodes.

It is not possible to know the generic characters of this species, and it is regrettable that Lambert erected a genus for it. I suspect that these specimens may be immature individuals of a species like *Clypeolampas leskei* (Goldfuss).

Lambert's drawings of the lectotype are inaccurate. According to his figures, the specimen appears to be well preserved and to have petals. I have included photographs of the lectotype (pl. 44, figs. 1-5). Mortensen (1948, text fig. 252) has reproduced Lambert's figures in his monograph but has labeled them as natural size when in reality they are twice natural size.

Durham and Melville (1957, p. 257) tentatively placed *Ovulechinus* with *Oligopygus* because of their general external similarity. However, bourrelets are present in *O. pilula*, and a floscelle was probably well developed in adult individuals. *Ovulechinus* is a cassiduloid, whereas *Oligopygus* is a holotypoid.

*Occurrence*.—Upper Cretaceous (Santonian) at Saint Paterne, France.

#### Genus PLATIPYGUS De Lorient

*Platipygus* De Lorient, 1902. Notes pour servir à l'étude des échinodermes, ser. 2, vol. 10, fasc. 1, p. 17. Type species by monotypy, *Cyrtoma posthumum* Ortmann.

*Remarks*.—I have been unable to locate any specimens of the type species and only known species of this genus. From De Lorient's figures this species looks very much like a *Stigmatopygus*. For this reason, Lambert and Thiéry and Mortensen considered *Platipygus*

a synonym of *Stigmatopygus*. However, all the other species of *Stigmatopygus* are from the Upper Cretaceous, whereas the type species of *Platypygus* is from the Miocene. As the phyllodes are not known in this species, it seems advisable to refer this genus to incertae sedis.

Mortensen and Lambert and Thiéry are mistaken in spelling *Platipygus* "Platypygus" and in turn considering it to be a junior homonym of *Platypygus* Loew 1844. It is spelled *Platipygus* in De Loriol's original description.

#### LITERATURE CITED

##### AGASSIZ, A.

- 1863. List of the echinoderms sent to different institutions in exchange for other specimens. Bull. Mus. Comp. Zool., vol. 1, No. 2, pp. 17-28.
- 1869. Preliminary report Echini, deep water Florida Straits. Bull. Mus. Comp. Zool., vol. 1, No. 9, pp. 253-308.
- 1872-1874. Revision of the Echini: Mem. Mus. Comp. Zool., vol. 3, pts. 3, 4, pp. 383-762, pls. 1-38.
- 1878. Report on the results of dredging . . . in the Gulf of Mexico by the U. S. Coast Survey Steamer "Blake." Report on the Echini. Bull. Mus. Comp. Zool., vol. 5, No. 9, pp. 185-196, 5 pls.
- 1883. Reports on the results of dredging in the Gulf of Mexico (1877-78) in the Caribbean Sea (1878-79) and along the Atlantic Coast of the United States (1880) by the U. S. Coast Survey Steamer "Blake." No. 24, pt. 1, Report on the Echini. Mem. Mus. Comp. Zool., vol. 10, No. 1, 126 pp., 32 pls.

##### AGASSIZ, L.

- 1836a. Notice sur les fossiles Crétacés du Jura Neuchatelois. Mém. Soc. Sci. Nat. Neuchâtel, vol. 1, pp. 126-145.
- 1836b. Prodrôme d'un monographie des radiaires ou échinodermes. Mem. Soc. Sci. Nat. Neuchâtel, vol. 1, pp. 168-199.
- 1839. Description des échinodermes fossiles de la Suisse: première partie. Allg. Schweizer. Ges. Neue Denkschr., vol. 1, 101 pp., pls. 1-13 bis.
- 1840a. Catalogus systematicus ectyporum echinodermatum fossilium musei Neocomensis, Solothurn. 20 pp.
- 1840b. Description des échinodermes fossiles de la Suisse: seconde partie. Allg. Schweizer. Ges. Neue Denkschr., Bd. 4, 108 pp., pls. 14-23.

##### AGASSIZ, L., and DESOR, P. J. E.

- 1847. Catalogue raisonné des échinides. Ann. Sci. Nat., ser. 3, vols. 6-8, 167 pp., 1 pl.

##### ARCHIAC, V. D'.

- 1850. Histoire des progrès de la géologie, vol. 3. 624 pp.

##### ARCHIAC, V. D', and HAIME, J.

- 1853. Description des animaux fossiles du groupe nummulitique de l'Inde, 373 pp., 36 pls., Paris.

##### ARNOLD, B. W., and CLARK, H. L.

- 1927. Jamaica fossil Echini; with descriptions of new species of Cainozoic Echinoidea by Herbert L. Hawkins. Mem. Mus. Comp. Zool., vol. 50, No. 1, 84 pp., 22 pls., 3 figs.

## BAJARUNAS.

1915. *Hysofygaster*, a new genus of sea-urchins from the Danian deposits of Mangyshlak. Geol. Vestnik-Petrograd, vol. 1, p. 230 (not seen).

## BECHE, H. T. DE LA.

1833. On *Echinoaus lampas*. Trans. Geol. Soc., ser. 2, vol. 1.

## BELL, F. J.

1880. On *Palacolampus*, a new genus of echinoid. Proc. Zool. Soc. London, vol. 18, pp. 43-49, pl. 4.

## BESAIRIE, H.

1930. Recherches géologiques à Madagascar. Contribution à l'étude des ressources minérales. Bull. Soc. Hist. Nat. Toulouse, vol. 60, pp. 345-616, pls. 1-27.

## BESAIRIE, H., and LAMBERT, J.

1930. Notes sur quelques échinides de Madagascar et du Zululand. Bull. Soc. Géol. France, vol. 30, pp. 107-116, pls. 4-10.

## BEURLÉN, K.

1933. Revision der Seeigel aus dem Norddeutschen Jura. Abb. Preuss. Geol. Landesanstalt, vol. 152, pp. 1-98, 16 figs.

## BITTNER.

1892. Ueber Echiniden des Tertiärs von Australien. Sitzungsber. Kais. Akad. Wiss., Math.-Nat. Classe, vol. 101, Bd. 3, pp. 331-371, pls. 1-4.

## BLAINVILLE, H. DE.

1830. Dictionnaire des sciences naturelles, Zoophytes, vol. 60.

## BRIGHTON, A. G.

1929. Tertiary irregular echinoids from the Chatham Islands, New Zealand. Trans. Proc. New Zealand Inst., vol. 60, pp. 308-319, pl. 30.

## CASTEX, L.

1930. Révision des échinides nummulitique du département des Landes. Act. Soc. Linn. Bordeaux, vol. 82, pp. 5-72, pls. 1-4.

## CHECCHIA-RISPOLI, G.

1914. Sopra alcuni Echinidi del Cretaceo superiore della Tripolitania raccolti dal cav. Ignazio Sanfilippo. Giorn. Sci. Nat. ed Econ., vol. 30, 14 pp., 1 pl.

1917. "Zuffardia," nuovo genere di Echinide del Senoniano della Tripolitania. Rend. Roy. Accad. Lincei, Cl. Sci. Mat. Nat., ser. 5a, vol. 26, fasc. 9, pp. 492-494.

1921. Fauna del Neocretaceo della Tripolitania, Echinidi. Mem. Descr. Carta Geol. d'Italia, vol. 8, 31 pp., 3 pls.

1931. Illustrazione di alcuni Echinidi del Maestrichtiano della Tripolitania raccolti da Ignazio Sanfilippo. Mem. Soc. Geol. Italiana, vol. 1, 25 pp., 2 pls.

1941. Sul genere "Pseudopygurus" Lambert. Reale Accad. d'Italia, Cl. Sci. Fis. Mat. Nat., ser. 7, vol. 2, fasc. 10, pp. 1-5, 1 fig.

1945. Di due nuovi generi di Echinidi del Cretaceo della Somalia. Boll. Ufficio Geol. d'Italia, vol. 68, 10 pp., 2 pls.

## CIFELLI, R.

1959. Bathonian Foraminifera of England. Bull. Mus. Comp. Zool., vol. 121, No. 7, pp. 265-368, 7 pls., 4 figs.

## CLARK, H. L.

1914. Hawaiian and other Pacific Echini: The Clypeastridae, Arachnoididae, Laganidae, Fibulariidae, and Scutellidae. *Mem. Mus. Comp. Zool.*, vol. 46, No. 1, 78 pp., pls. 122-143.
1917. The Echinoneidae, Nucleolitidae, Urechinidae, Echinocorythidae, Calymnidae, Pourtalesiidae, Paleostomatidae, Aeropsidae, Palaeopneustidae, Hemiasteridae, and Spatangidae. *Idem*, No. 2, pp. 85-283, pls. 144-161.
1923. Two new genera of sea-urchins. *Bull. Mus. Comp. Zool.*, vol. 65, pp. 341-348.

## CLARK, W. B., and TWITCHELL, M. W.

1915. The Mesozoic and Cenozoic Echinodermata of the United States. *U. S. Geol. Surv. Monogr.* 54, 341 pp., 108 pls.

## CLAUS, C.

1880. *Grundzüge der Zoologie*, 4th ed., vol. 1, 822 pp. (Marburg and Leipzig).

## COLLIGNON, M.

1930. Beitrag zur Kenntnis der eozänen Echiniden-fauna des Krappfeldes (Kärnten). *Jahrb. Geol. Bundesanstalt, Wien*, vol. 80, pp. 541-570, pls. 31-33.

## CONRAD, T. A.

1850. Descriptions of one new Cretaceous and seven new Eocene fossils. *Journ. Acad. Nat. Sci. Philadelphia*, ser. 2, vol. 2, pp. 39-41, illus.

## COOKE, C. W.

1942. Cenozoic irregular echinoids of eastern United States. *Journ. Paleont.*, vol. 16, No. 1, pp. 1-62, pls. 1-8.
1946. Comanche echinoids. *Journ. Paleont.*, vol. 20, No. 3, pp. 193-237, 4 pls.
1953. American Upper Cretaceous Echinoidea. *U. S. Geol. Surv. Prof. Pap.* 254-A, pp. 1-44, pls. 1-16.
1955. Some Cretaceous echinoids from the Americas. *U. S. Geol. Surv. Prof. Pap.* 264-E, pp. 87-112, pls. 18-29.
1959. Cenozoic echinoids of eastern United States. *Geol. Surv. Prof. Pap.* 321, 106 pp., 43 pls.
1961. Cenozoic and Cretaceous echinoids from Trinidad and Venezuela. *Smithsonian Misc. Coll.*, vol. 142, No. 4, Publ. 4459, 35 pp., 14 pls.

## COQUAND, M. H.

1862. Géologie et paléontologie de la région sud de la Provence de Constantine. *Mém. Soc. Emulation de la Provence*, vol. 2, pp. 5-342, 59 figs.

## COSSMAN, M.

1901. *Revue critique de paléozoologie*, vol. 5, p. 58.

## COTTEAU, G.

- 1849-1856. Études sur les échinides fossiles du Département de L'Yonne, vol. 1, terrain Jurassique, 347 pp., 46 pls. Paris.
1851. Catalogue méthodique des échinides neocomiens de L'Yonne. *Bull. Soc. Sci. Hist. Nat. Yonne*, vol. 5.
1856. Sur les échinides fossiles de la Sarthe. *Bull. Soc. Géol. France*, ser. 2, vol. 13.



- 1857-1878. Études sur les échinides fossiles du Département de L'Yonne, vol. 2, terrain Crétacé, 518 pp., pls. 47-84. Paris.
1860. Échinides irréguliers paléontologie française, terrain Crétacé, ser. 1, vol. 6, pp. 433-596, pls. 909-1006.
1863. Échinides fossiles des Pyrénées. Congrès Sci. France, Sess. de Bordeaux.
1866. Échinides nouveaux ou peu connus. Rev. Mag. Zool., ser. 2, vol. 18, pp. 262-268, pl. 14.
- 1867-1874. Échinides irréguliers paléontologie française, ser. 1, vol. 9, terrain Jurassique, 551 pp., 142 pls. Paris.
1869. Échinides nouveaux ou peu connus. Rev. Mag. Zool., ser. 2, vol. 21, pp. 238-248.
1880. Description des échinides tertiaires de Belgique. Mém. Acad. Roy. Sci., Lett. et Beaux-arts de Belgique, vol. 43, 90 pp. 6 pls.
1883. Échinides nouveaux ou peu connus. Bull. Soc. Zool. France, vol. 8, pp. 450-464, pls. 14, 15.
1885. Échinides nouveaux ou peu connus. Bull. Soc. Zool. France, vol. 9, pp. 328-342, pls. 10, 11.
- 1885-1894. Paléontologie française ou description des fossiles de la France, terrain Tertiaire, échinides Éocènes, 2 vols.: vol. 1, 672 pp., pls. 1-200, 1885-1889; vol. 2, 788 pp., pls. 200-384, 1889-1894.
1894. Sur quelques espèces d'échinides du Liban. Assoc. Franc. Avanc. Sci., Congr. de Besançon, vol. 22, pp. 346-360, pls. 1, 2.
- COTTEAU, G., and GAUTHIER, V.
1895. Mission scientifique en Perse par J. de Morgan. Vol. 3, Études géologiques, pt. 2, Paléontologie, 107 pp., 16 pls. Paris.
- COTTEAU, G., and LEYMERIE.
1856. Catalogue des échinides fossiles des Pyrénées. Bull. Soc. Géol. France, ser. 2, vol. 13, pp. 319-354.
- COTTEAU, G.; PERON, P. A.; and GAUTHIER, V.
- 1876-1884. Échinides fossiles de l'Algérie, vol. 1, Paris. Fasc. 1, 1883, Terrain Jurassique, 79 pp., 8 pls.; fasc. 2, 1884, Étages Tithonique et Neocomien, 99 pp., 9 pls.; fasc. 3, 1876, Étages Urgo-aptien et Albien, 90 pp., 8 pls.; fasc. 4, 1878, Étage Cenomanien, pp. 1-144, pls. 1-8; fasc. 5, 1879, Étage Cenomanien (concluded), pp. 145-234, pls. 9-16.
- COTTEAU, G., and TRIGER, JULES.
- 1855-1869. Échinides du Département de la Sarthe considérés au point de vue zoologique et stratigraphique. 455 pp., 65 pls. Paris.
- CURRIE, E.
1925. The collection of fossils and rocks from Somaliland. Pt. 5, Jurassic and Eocene Echinoidea. Monogr. Geol. Dept. Hunterian Mus., Glasgow Univ., pp. 46-76, pls. 8-10.
1927. Jurassic and Eocene Echinoidea from Somaliland. Trans. Roy. Soc. Edinburgh, vol. 55, pt. 2 (No. 18), pp. 411-441, 1 pl., 7 text figs.
- DAMES.
1878. Die Echiniden der Vicentinischen und Veronesischen tertiarablagerungen. Palaeontographica, vol. 25.
- DAS-GUPTA, H. C.
1921. A short note on the Cretaceous echinoid *Cyrtoma*, M'Clelland. Journ. Asiatic Soc. Bengal, Calcutta, vol. 16, pp. 297-300.

## DEFRANCE.

1825. Dictionnaire des sciences naturelles.

## DEMOLY, and LAMBERT, J.

1913. Nouvelles observations sur les échinides de la Savoie. Bull. Soc. Hist. Nat. Savoie, 1912. Chambéry.

## DESMOULINS, C.

1835-1837. Études sur les échinides. 520 pp. Bordeaux.

## DESOR, EDOUARD.

1842. Des galérites: Monographies d'échinodermes vivans et fossiles, par Louis Agassiz, Monogr. 3, iv+94 pp., 13 pls.

1855-1858. Synopsis des échinides fossiles. 490 pp., 44 pls., Paris, Wiesbaden.

## DUNCAN, P. M.

1891. A revision of the genera and great groups of the Echinoidea. Journ. Linnean Soc. (Zool.), vol. 23, 311 pp.

## DUNCAN, P. M., and SLADEN, W. P.

1882-1886. Fossil Echinoidea of Western Sind and the coast of Bîlûchistân and of the Persian Gulf, from the Tertiary formations. Palaeontologia Indica, ser. 14, vol. 1, pt. 3, 382 pp., 58 pls.

## DURIHAM, J. W.

1955. Classification of clypeastroid echinoids. Univ. California Publ. Geol. Sci., vol. 31, No. 4, pp. 73-198, 38 text figs., pls. 3, 4.

1959. Palaeoclimates. In Physics and chemistry of the earth, vol. 3, pp. 1-16. Pergamon Press, London.

## DURIHAM, J. W., and MELVILLE, R. V.

1957. A classification of echinoids. Journ. Palcont., vol. 31, No. 1, pp. 242-272, 9 figs.

## EBRAY, TH.

1858. Note sur un nouveau genre d'échinoderme. Bull. Soc. Géol. France, ser. 2, vol. 15, pp. 482-484, 1 fig.

1859. Note sur le genre *Galeroptygus* et étude des plaques interapicales chez les Collyrites. Bull. Soc. Géol. France, ser. 2, vol. 16, pp. 759-763.

## EMMONS, EBENEZER.

1858. Agriculture of the eastern counties, together with descriptions of the fossils of the marl beds. North Carolina Geol. Surv. Rep., xvi+314 pp., illus.

## ENGEL, H., and MEIJER, M.

1957. Notes sur les échinides du tuffeau de Maastricht (Maastrichtien, Dumont, 1849). Overdruk Natuurhist. Maandblad, 46c, pp. 88-94, 1 pl., 4 figs.

## ETALLON.

1859. Études paléontologiques sur le Ht-Jura; rayonnés du Corallien. Mem. Soc. Emulation de Montbéliard, vol. 3 (1858).

## FISCHER, A. G.

1951. The echinoid fauna of the Inglis member, Moody Branch formation. Florida Geol. Surv. Geol. Bull. 34, pt. 2, pp. 47-101, 7 pls.

## FORBES, E.

1846. Report on the fossil Invertebrata from southern India, collected by Mr. Kaye and Mr. Cunliffe. 174 pp., pls. 7-19 (plates published in 1856). Trans. Geol. Soc. London, ser. 2, vol. 7, pp. 97-174.

1849. Memoirs of the Geological Survey of the United Kingdom, decade 1.

## FOURTAU, R.

1899. Révision des échinides fossiles de l'Égypte. Mém. Inst. Égypt., vol. 3, fasc. 8.
1909. Note sur les échinides fossiles recueillis par M. Teilhard de Chardin dans l'Éocène des environs de Minieh. Bull. Inst. Égypt., ser. 5, vol. 2, pp. 122-155, pls. 8-9.
1913. Notes sur les échinides fossiles de l'Égypte. Bull. Inst. Égypt., ser. 5, vol. 7, pp. 62-71, pl. 7.
1914. Catalogue des invertébrés fossiles de l'Égypte représentés dans les collections du Musée de Géologie au Caire, terrains Crétacés, pt. 1, Échinodermes, 109 pp., 8 pls.
1920. Catalogue des invertébrés fossiles de l'Égypte représentés dans collections du Musée de Géologie au Caire, terrains Tertiaires, pt. 2, Échinodermes Neogenes. Geol. Surv. Egypt. Pal., ser. 4, 100 pp., 4 pls.
1921. Catalogue des invertébrés fossiles de l'Égypte représentés dans les collections du Musée de Géologie au Caire, terrains Crétacés, pt. 3, Échinodermes (Supplément). Geol. Surv. Egypt. Pal., ser. 5, 101 pp., 11 pls.
1924. Catalogue des invertébrés fossiles de l'Égypte représentés dans les collections du Musée de Géologie au Caire, terrains Jurassiques, pt. 1, Échinodermes. Geol. Surv. Egypt. Pal., ser. 6, 39 pp., 5 pls.

## GAUTHIER, V.

- 1889a. Description des échinides fossiles recueillis en 1885 et 1886, dans la région sud des hauts plateaux de la Tunisie, par M. Philippe Thomas, 116 pp., 6 pls.
- 1889b. Description des échinides recueillis par M. Thomas en Tunisie. Bull. Soc. Géol. France, ser. 3, tome 18, pp. 136-144.

## GAUTHIER, V., in COTTEAU, PERON, GAUTHIER.

1885. Échinides fossiles de l'Algérie, vol. 9, Étage Éocène, 9 pls.

## GAUTHIER, V., in FOURTAU, R.

1899. Révision des échinides fossiles de l'Égypte. Mém. Inst. Égypt., tome 3, pp. 605-740, 4 pls.

## GMELIN, J. F.

1789. Caroli Linnaei Systema Naturae.

## GOLDFUSS, A.

- 1826-1844. Petrefacta Germaniae. Abbildungen und Beschreibungen Petrefacten Deutschlands . . . Theil 1-3 in 2 vols. Düsseldorf.

## GORDON, I.

1929. Skeletal development in *Arbacia*, *Echinarachnius* and *Leptasterias*. Philos. Trans. Roy. Soc. London, ser. B, vol. 217, pp. 289-334, 26 figs.

## GORODISKI, A.

1951. Au sujet de quelques Cassiduloida (oursins irréguliers) de l'Éocène Moyen du Sénégal. Bull. Mus. Hist. Nat. Paris, ser. 2, vol. 23, pp. 322-330, 1 pl.

## GRANT, U. S., and HERTLEIN, L. G.

1938. The West American Cenozoic Echinoidea. Publ. Univ. California, vol. 2, 225 pp., 30 pls., 17 figs.

## GRAY, J. E.

1825. An attempt to divide the Echinida, or sea eggs, into natural families. *Ann. Philos.*, vol. 26, pp. 423-431.
1851. New genera and species of Scutellidae and Echinolampidae. *Proc. Zol. Soc. London*, vol. 19, pp. 34-38.

## GREGORY, J. W.

1890. Some additions to the Australian Tertiary Echinodermata. *Geol. Mag.*, n.s., dec. 3, vol. 7, No. 11, pp. 481-492, pls. 13, 14.
1891. The Maltese fossil echinoids and their evidence of the correlation of the Maltese rocks. *Trans. Roy. Soc. Edinburgh*, vol. 36, pt. 3, No. 22, pp. 585-639, 2 pls.

## GROOT, J. J.; ORGANIST, D. M.; and RICHARDS, H. G.

1954. Marine Upper Cretaceous formations of the Chesapeake and Delaware Canal. *Delaware Geol. Surv. Bull.* No. 3, 62 pp.

## HAWKINS, H.

1911. On the structure and evolution of the phyllodes in some fossil Echinoidea. *Geol. Mag.*, dec. 5, vol. 8, pp. 257-265, pl. 13.
- 1920a. The morphology and evolution of the ambulacrum in the Echinoidea Holoctypoida. *Philos. Trans. Roy. Soc. London*, ser. B, vol. 209, pp. 377-480, pls. 61-69.
- 1920b. Morphological studies on the Echinoidea Holoctypoida and their allies, No. 10, on *Apatopygus* gen. nov. and the affinities of some Recent Nucleolitoida and Cassiduloida. *Geol. Mag.*, vol. 57, pp. 393-401, pl. 7.

## HYMAN, L. H.

1955. The invertebrates, vol. 4: Echinodermata. The Coelomate Bilateria, 763 pp., 280 figs. New York.

## IKINS, W. C.

1940. Some echinoids from the Cretaceous of Texas. *Bull. Amer. Paleontology*, Ithaca, vol. 25, pp. 49(1)-88(40), pls. 4(1)-7(4).

## JEANNET, A.

1928. Contribution à l'étude des échinides tertiaires de la Trinité et du Venezuela. *Soc. Paléont. Suisse Mém.*, vol. 48, 49 pp., 6 pls.

## JOYSEY, K.

1952. Note on the Corallian echinoid *Pygurus hausmanni* (Koch and Dunker) from the Yorkshire Wolds. *Proc. Geol. Assoc. London*, vol. 63, pp. 240-243, pl. 9.

## KEW, W. S. W.

1920. Cretaceous and Cenozoic Echinoidea of the Pacific Coast of North America. *Univ. California Publ. Geol.*, vol. 12, No. 2, pp. 23-236, pls. 3-42, 5 text figs.

## KIER, P. M.

1957. Tertiary Echinoidea from British Somaliland. *Journ. Paleont.*, vol. 31, No. 5, pp. 839-902, 5 pls., 20 text figs.

## KONGIEL, R.

1935. Contribution à l'étude du "siwak" dans les environs de Pulawy (plateau de Lublin). *Trav. Inst. Géol. et Geogr. l'Univ. Wilno*, 59 pp., 11 pls.



## LAMARCK, J. B.

1801. Système des animaux sans vertèbres. 432 pp.

1816. Animaux sans vertèbres, vol. 3.

## LAMBERT, J.

1892. Recherches sur les échinides de l'Aptien de Grandpré. Bull. Soc. Géol. France, ser. 3, vol. 20, pp. 38-100, pls. 2-4.

1898. Notes sur les échinides de la Craie de Ciply. Bull. Soc. Belge Géol., ser. 2, vol. 11.

1899. Revue critique palaeozoologie, 3d année, p. 119.

1902. Description des échinides fossiles de la Province de Barcelone. Mém. Soc. Géol. France, vol. 24, pp. 1-58.

1904. Note sur quelques échinides du Barremien du Gard. Bull. Soc. Géol. France, ser. 4, vol. 4, pp. 841-846, 2 figs.

1905a. *In* Doncieux, Fossiles nummulitiques de l'Aube et de l'Hérault. Ann. Univ. Lyon, fasc. 17, pp. 129-164, pl. 5.

1905b. Échinides du sud de la Tunisie (environs de Tatahouine). Bull. Soc. Géol. France, ser. 4, vol. 5, pp. 569-577, pl. 22.

1906. Étude sur les échinides de la Molasse de Vence. Ann. Soc. Lett., Sci., Arts Alpes-Maritimes, vol. 20, 64 pp., 10 pls. Nice.

1909. Liste critique des échinides du Calcaire à Baculites du Cotentin. Bull. Soc. Linn. Normandie, ser. 6, vol. 2, pp. 3-30, pl. 1.

1911a. *In* Lemoine, Contributions à la géologie des colonies francaises, 2, Sur deux oursins nouveaux du Jurassique de Madagascar. Bull. Soc. Géol. France, ser. 4, vol. 7.

1911b. Notes sur quelques échinides Éocènes des Corbières Septentrionales. Ann. Univ. Lyon, ser. 1, vol. 30, pp. 165-199, pl. 16.

1911c. Description des échinides Crétacés de la Belgique principalement de ceux conservés au Musée Royal de Bruxelles, échinides de l'étage Senonien, Bruxelles. 81 pp., 3 pls.

1913. Description des échinides des terrains Neogenes du Bassin du Rhone. Mém. Soc. Paleont. Suisse, vol. 39, pp. 105-151, 5 pls.

1914. Revue critique palaeozoologie, vol. 18, p. 112.

1916a. Revue critique palaeozoologie, vol. 20, pp. 168-171.

1916b. Sur l'existence de l'étage Valangien dans l'Aube et dans l'Yonne (avec observations sur les échinides). Mém. Soc. Acad. Aube, vol. 80, Troyes, pp. 19-94.

1918. Considerations sur la classification des échinides atelostomes. Mém. Soc. Acad. Aube, ser. 3, vol. 55, pp. 9-54.

1920a. Sur quelques genres nouveaux d'échinides. Mém. Soc. Acad. Aube, vol. 84, pp. 145-172, 2 pls.

1920b. Revue critique de paléozoologie, vol. 24, p. 138.

1920c. Échinides fossiles des environs de Santander. Ann. Soc. Linn. Lyon, vol. 66 (1919), pp. 1-32, pls. 1-3.

1927. Révision des échinides fossiles de la Catalogne. Mus. Cienc. Nat. Barcelona, Memórias, geol. ser., vol. 1, No. 1, 102 pp., 4 pls.

1931. Étude sur les échinides fossiles du Nord de l'Afrique. Mém. Soc. Géol. France, vol. 7, fasc. 2, 108 pp., 4 pls.

1932. Étude sur les échinides fossiles du Nord de l'Afrique. Mém. Soc. Géol. France, vol. 7, fasc. 4, pp. 109-228, pls. 5-8.

1935. Note sur les échinides Jurassiques et les oscillations duetroit poitevin. Bull. Soc. Géol. France, ser. 5, vol. 4, pp. 523-536, pls. 26-27.
1936. Quelques nouveaux échinides fossiles du Crétacé du Mexique. Bull. Soc. Géol. France, ser. 5, vol. 6, pp. 3-6, pl. 1.
1937. Échinides fossiles du Maroc. Notes Mém. Serv. Mines, Carte Géol. Maroc, vol. 39, pp. 39-109, pls. 1-4, 4 figs.
- LAMBERT, J., and JEANNET, A.
1928. Nouveau catalogue des moules d'échinides fossiles du Musée d'Histoire Naturelle de Neuchâtel. Mém. Soc. Helvétique Sci. Nat., vol. 64, Mém. 2, pp. 83-233, 2 pls.
- LAMBERT, J., and THIÉRY, P.
- 1909-1925. Essai de nomenclature raisonnés des échinides. 607 pp., 15 pls. Chaumont.
- LAUBE, G. C.
1868. Ein Beitrag zur kenntniss der Echinodermen des Vicentinischen Tertiärgebietes. Sitzungsab. Kais. Akad. Wiss., Math.-Nat., vol. 29, pp. 1-38.
- LEES, G. M.
1928. The geology and tectonics of Oman and parts of southeastern Arabia. Quart. Journ. Geol. Soc. London, vol. 74, pp. 585-670, pls. 41-51.
- LESKE, N. G.
1778. Klein's Naturalis dispositio echinodermatum. 278 pp., 54 pls.
- LORIOL, P. DE.
1873. Échinologie Helvétique, description des oursins fossiles de la Suisse, pt. 2, Échinides de la période Crétacée. 398 pp., 33 pls.
1880. Monographie des échinides contenus dans les Couches Nummulitiques de l'Égypte. Mém. Soc. Phys. Hist. Nat. Genève, vol. 27, pp. 59-148, 11 pls.
1888. Description des échinides de la province d'Angola. Mém. Soc. Phys. Hist. Nat. Genève, vol. 30.
1899. Notes pour servir à l'étude des échinodermes, vol. 7. Mém. Soc. Phys. Hist. Nat. Genève, vol. 33, pt. 2, No. 1, pp. 3-34, 3 pls.
1900. Notes pour servir à l'étude échinodermes, vol. 8. Rev. Suisse Zool., vol. 8, pp. 55-96, pls. 6-9.
1901. Notes pour servir à l'étude des échinodermes, vol. 9, 45 pp., 3 pls.
1902. Notes pour servir à l'étude des échinodermes, vol. 10, 32 pp., 4 pls.
- MACBRIDE, E. W.
1906. Echinodermata. In The Cambridge Natural History, ed. S. F. Harmer and A. E. Shipley, vol. 1, ch. 16-21, pp. 425-623, figs. 185-296. London.
- MACCAGNO, A. M.
1947. Illustrazione degli echinidi giurassici della Somalia. Atti Accad. Naz. Lincei Mem., ser. 8, vol. 1, pp. 99-136, 1 pl.
- MAURY, C. J.
- 1934a. *Lovenilampas*, a new echinoderm genus from the Cretaceous of Brazil. Amer. Mus. Nov. No. 744, pp. 1-5, 1 fig.
- 1934b. Fossil invertebrata from northeastern Brazil. Bull. Amer. Mus. Nat. Hist., vol. 67, pp. 123-179, pls. 9-19.

M'CLELLAND, J.

1840. On *Cyrtoma* a new genus of fossil Echinida. Calcutta Journ. Nat. Hist., vol. 1, No. 2, pp. 155-187, pls. 4-6.

MCCRADY, J.

1859. Remarks on the Eocene formation in the neighborhood of Alligator, Florida. Proc. Elliott Soc. Nat. Hist., Charleston, S. C., vol. 1, pp. 282-283.

MELVILLE, R. V.

1952. On a new species of irregular echinoid (*Plagiochasma corxwellense* sp. nov.) from the Lower Greensand of Faringdon, Berks. Bull. Geol. Surv. Great Britain, No. 4, pp. 1-7, 1 pl., 1 fig.

MICHELIN, HARDOUIN.

1850. Notice sur deux espèces d'échinides fossiles. Rev. et Mag. Zool., ser. 2, vol. 2, pp. 240, 241.

MILLET, P. A.

1854. Paléontologie de Maine-et-Loire.  
1865. Indicateur de Maine-et-Loire, vol. 2, 616 pp.

MORTENSEN, T.

1922. Echinoderms of New Zealand and the Auckland-Campbell Islands. Vid. Medd. Nat. Forsch., vol. 73, pp. 139-198, pls. 6-8.  
1948. A monograph of the Echinoidea, vol. 4. pt. 1, Holactypoida, Cassiduloida. 371 pp., 14 pls., 326 text figs. Copenhagen.

MORTON, S. G.

1834. Synopsis of the organic remains of the Cretaceous group of the United States. 88 pp., 19 pls. Philadelphia. Reprinted from Amer. Journ. Sci., vols. 17, 18, 1830.

MUNIER-CHALMAS, E.

1882. In Hebert, Sur le groupe nummulitique du midi de la France. Bull. Soc. Géol. France, ser. 3, vol. 10, p. 369 (genre *Oriolampas*).

NEAVE, S. A.

1939. Nomenclator Zoologicus, vol. 1, 957 pp. Published by the Zoological Society of London.

NICHOLS, D.

1959. Changes in the Chalk heart-urchin *Micraster* interpreted in relation to living forms. Philos. Trans. Roy. Soc. London, vol. 242, pp. 347-437, 1 pl., 46 figs., 13 tables.

ORBIGNY, ALCIDE D'.

- 1854-1860. Échinoides irreguliers: Paléontologie française, terrain Crétacé, ser. 1, vol. 6, 596 pp., pls. 801-1006. (Completed by G. Cotteau.)

PENECKE, K. A.

1885. Das Eocän des Krappfeldes in Kapten. Sitzungsab. Kais. Akad. Wiss., vol. 90, pp. 327-371.

PETITOT, M. L.

1954. Sur une nouvelle espèce d'échinide irrégulier du Maroc: *Pseudopygurus ambroggii* nov. sp. Notes Serv. Mines Maroc, vol. 121, pp. 83-87, 1 pl., 2 figs.

POMEL, N. A.

1869. Revue des échinodermes et de leur classification pour servir d'introduction à l'étude des fossiles. Paris.

1883. Classification méthodique et genera des échinides vivants et fossiles. 131 pp., 1 pl. Alger.
1887. Paléontologie ou description des animaux fossiles de l'Algérie, échinodermes.
1888. Notes d'échinologie synonymique. Bull. Soc. Géol. France, ser. 3, vol. 16, pp. 441-453.
- RAVENEL, E.
1848. Echinidae, Recent and fossil, of South Carolina. 4 pp., 10 figs. Charleston, S. C.
- ROMAN, J.
1955. Sur le genre *Echinolampas*. Bull. Soc. Géol. France, ser. 6, vol. 4, pp. 689-699, 2 text figs.
- SANTOS, M. E. C. M.
1958. Equinóides Miocênicos da Formação Pirabas. Bull. 179, Ministério da Agricultura, Divisão de Geologia e Mineralogia, Rio de Janeiro, 24 pp., 5 pls.
- SAVIN, L.
1902. Notes sur quelques échinides du Dauphiné. Bull. Soc. Stat. l'Isère, ser. 4, vol. 6.
- SCHLÜTER, CL.
1902. Zur Gattung Caratomus (Anhang). Zeitschr. Deutsch. Geol. Ges., vol. 54, pp. 302-335, pls. 11, 12.
- SHERBORN, C. D.
1940. Where is the ——— Collection? 148 pp. Cambridge University Press.
- SLOCOM, A. W.
1909. New echinoids from the Ripley group of Mississippi. Field Mus. Nat. Hist. Publ. 134 (Geol. ser., vol. 4, No. 1), 16 pp., 3 pls.
- SMISER, J. S.
1935. A monograph of the Belgian Cretaceous echinoids. Mus. Roy. Hist. Nat. Belgique Mém. No. 68, 98 pp., 9 pls.
- STEPHENSON, L. W., ET AL.
1942. Correlation of the outcropping Cretaceous formations of the Atlantic and Gulf Coastal Plain and trans-Pecos Texas. Bull. Geol. Soc. Amer., vol. 53, No. 3, pp. 435-448, illus.
- STOLICZKA, F.
1873. The Cretaceous fauna of southern India, the Echinodermata. Mem. Geol. Soc. India, ser. 8, vol. 4, No. 3, 59 pp., 7 pls.
- SZÖRÉNYI, E.
1953. Moizane Echinoiden aus den westlichen teilen der Ukraine. Geol. Hung., ser. Palaeont., vol. 23, pp. 1-104, 8 pls. German translation pp. 49-102.
- 1955a. Échinides Crétacés de la Bakony. Geol. Hung., ser. Palaeont., vol. 26, 286 pp., 22 pls. French translation pp. 149-286.
- 1955b. Notes pour servir à l'étude des Archiacia (Échinides): Acta Geol. Hung., vol. 3, fasc. 4, pp. 383-392, 9 text figs.
- TESSIER, F.
1952. Contributions à la stratigraphie et à la paléontologie de la partie ouest du Senegal (Crétacé et Tertiaire). Gouv. gen. A.O.F. Bull. Dir. Mines, No. 14, pp. 291-311, pls. 15-18.



## WEISBORD, N. E.

1934. Some Cretaceous and Tertiary echinoids from Cuba. Bull. Amer. Paleont., vol. 20, No. 70C, pp. 167 165(1)-266 (102), pls. 20(1)-28(9).

## WRIGHT, T. W.

1851. On the Cassidulidae of the oolites, with descriptions of some new species of that family. Ann. Mag. Nat. Hist., ser. 2, vol. 9.
1855. On fossil echinoderms from the Island of Malta; with notes on the stratigraphical distribution of the fossil organisms in the Maltese beds. Ann. Mag. Nat. Hist., ser. 2, vol. 15, pp. 101-127, 175-196, 262-277, pls. 4-7.
- 1855-1878. Monograph on the British fossil Echinodermata of the oolitic formations, vol. 1, the Echinoidea, 481 pp., 43 pls. London.
- 1864-1882. Monograph of the British fossil Echinodermata from the Cretaceous formations. Palaeont. Soc. Monogr., 371 pp., 80 pls.

## ZÁZVORKA, V.

1953. *Trematopygus novaki* sp. n. (Echinoidea) from the Upper Cretaceous of Bohemia. Mém. Soc. Sci. Bohème, vol. 11 (1952), pp. 1-5, 1 pl.

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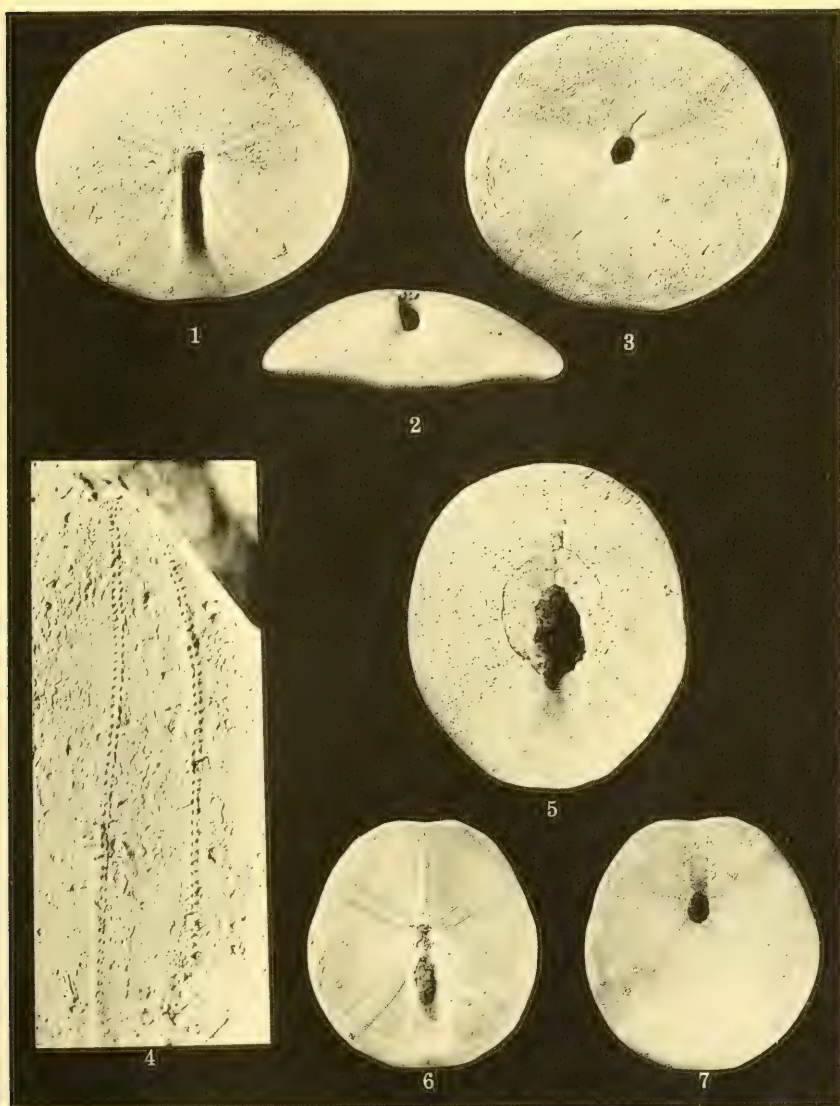
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## PLATES

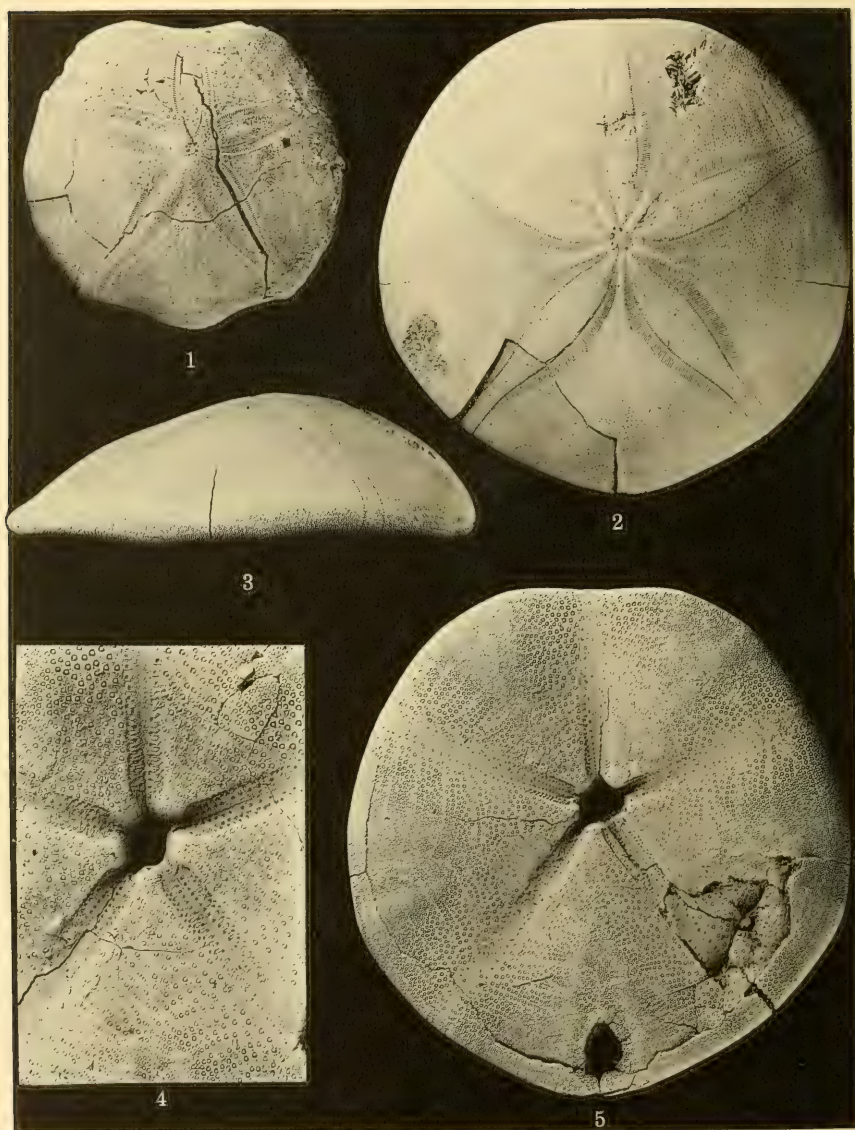






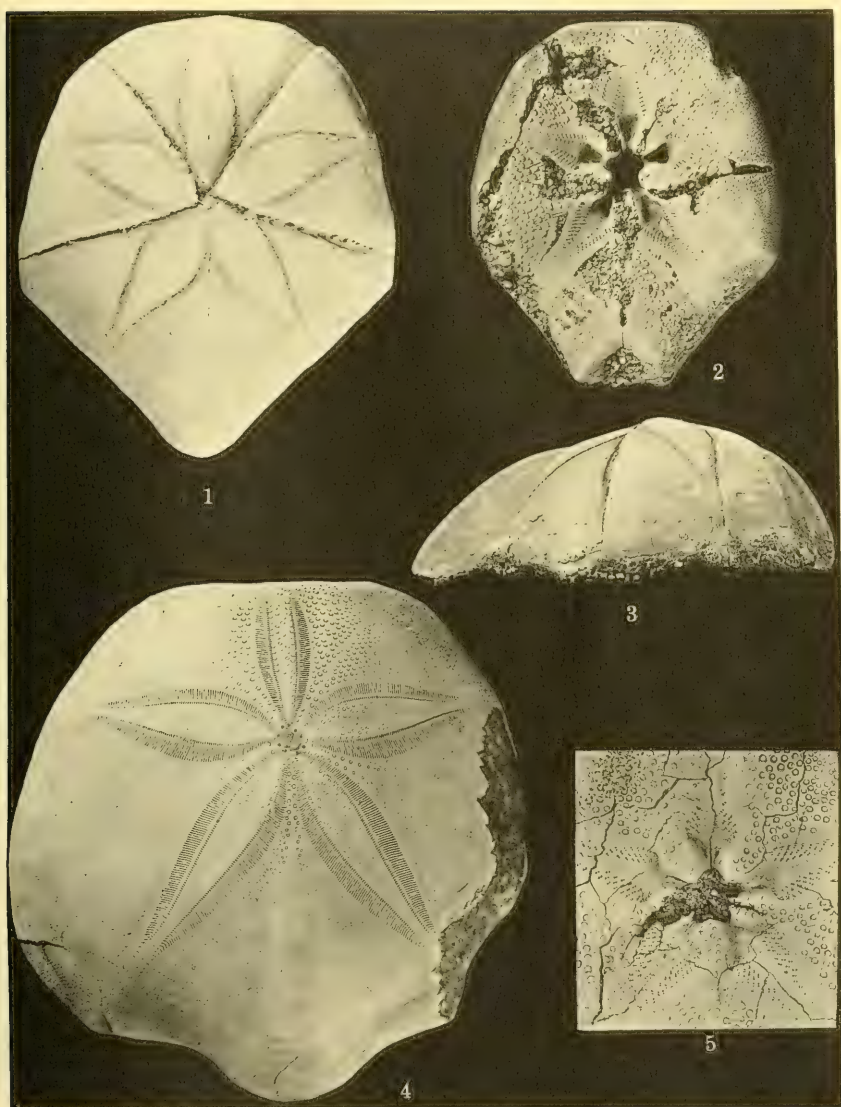
1-4, *GALEROPYGUS AGARICIFORMIS* (WRIGHT); 5, *HYBOCLYPUS CAUDATUS* WRIGHT; 6, 7, *HYBOCLYPUS GIBBERULUS* AGASSIZ

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1, *Pygurus* (*Pygurus*) *montmollini* Agassiz; 2-5, *Pygurus* (*Mepygurus*) *depressus* Agassiz

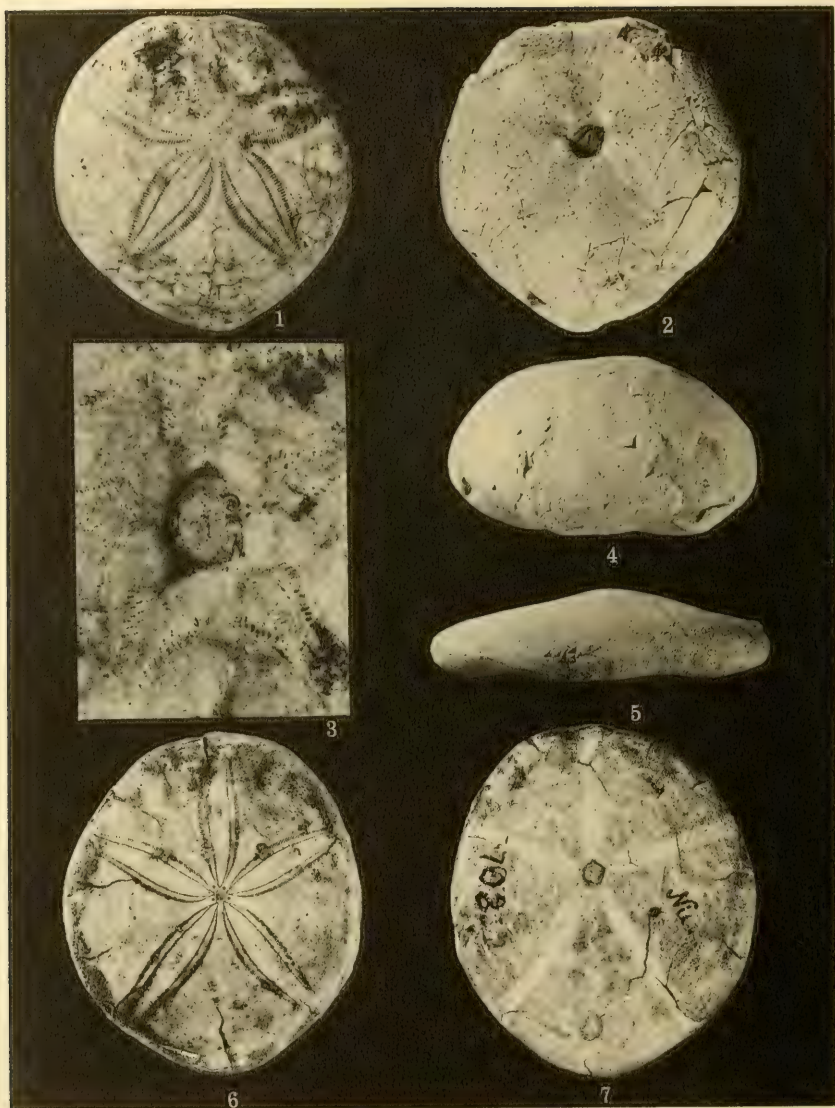
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1-3, *Pygurus (Pygurus) Lampas* (De la Beche); 4, *Pygurus (Pygurus) Blumenbachi* Kock and Dunker; 5, *Pygurus (Pygurus) rostratus* Agassiz

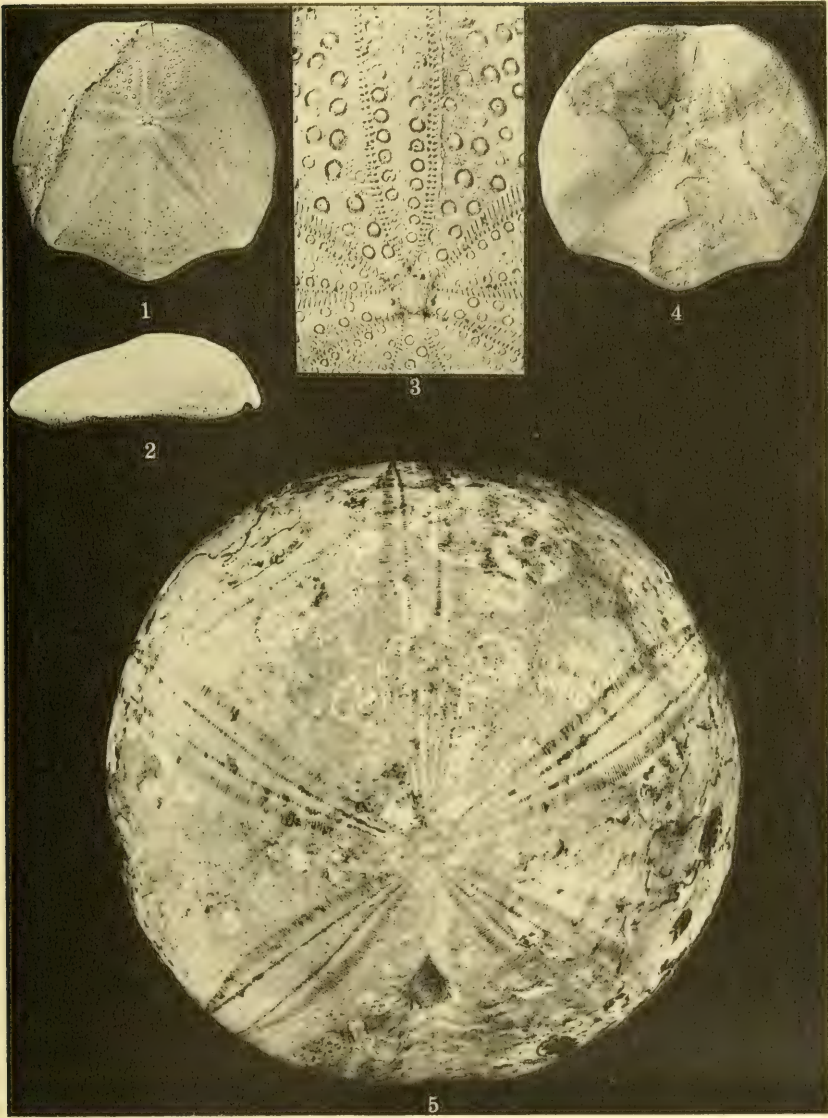
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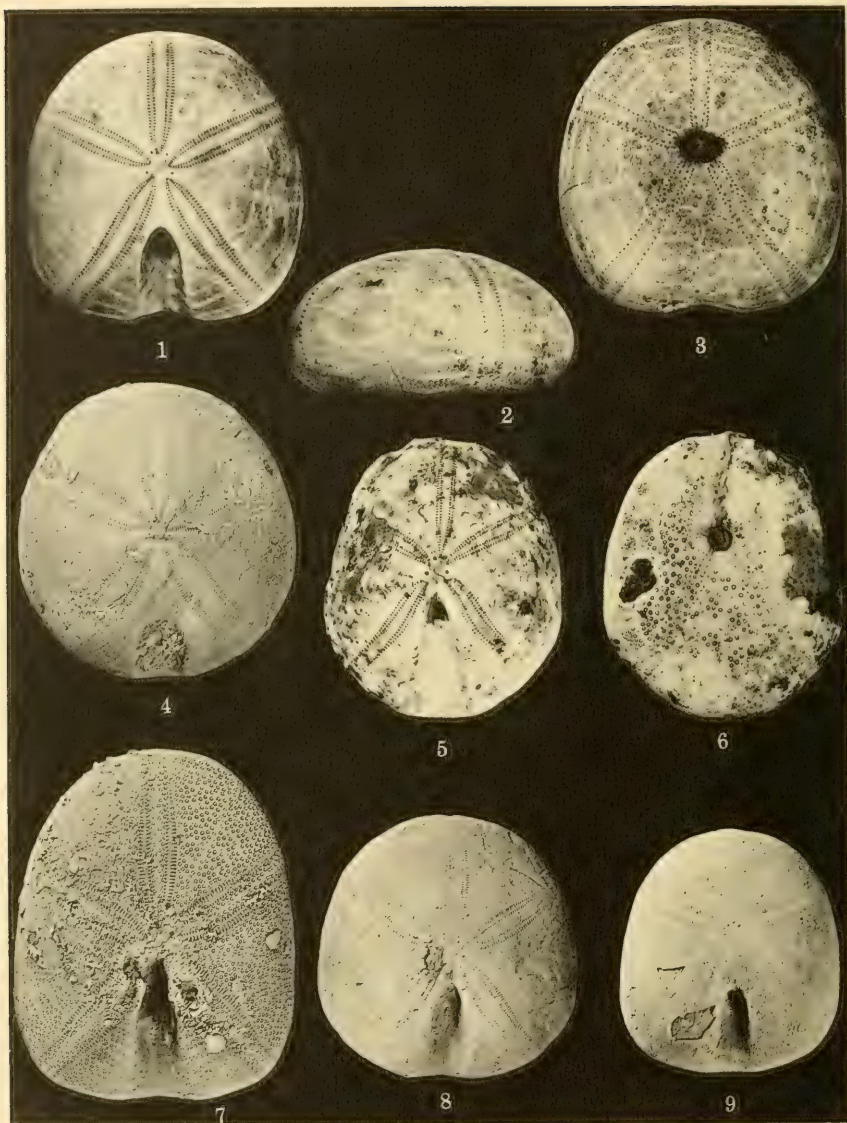
1-4, *PYGURUS* (*PYGUROPSIS*) *NOETLINGI* DE LORIOL;  
5-7, *ASTROLAMPAS PRODUCTUS* (AGASSIZ)

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-4, *PSEUDOPYGURUS LETTERONI* LAMBERT; 5, *CLYPEUS AGASSIZI* (WRIGHT)

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-3, *NUCLEOLITES SCUTATUS* LAMARCK; 4, *NUCLEOLITES HUGI* (AGASSIZ); 5, 6, *NUCLEOLITES GRACILIS* AGASSIZ;  
7, *NUCLEOLITES ELONGATUS* AGASSIZ; 8, *NUCLEOLITES AMPLUS* AGASSIZ; 9, *NUCLEOLITES SUBQUADRATUS* AGASSIZ

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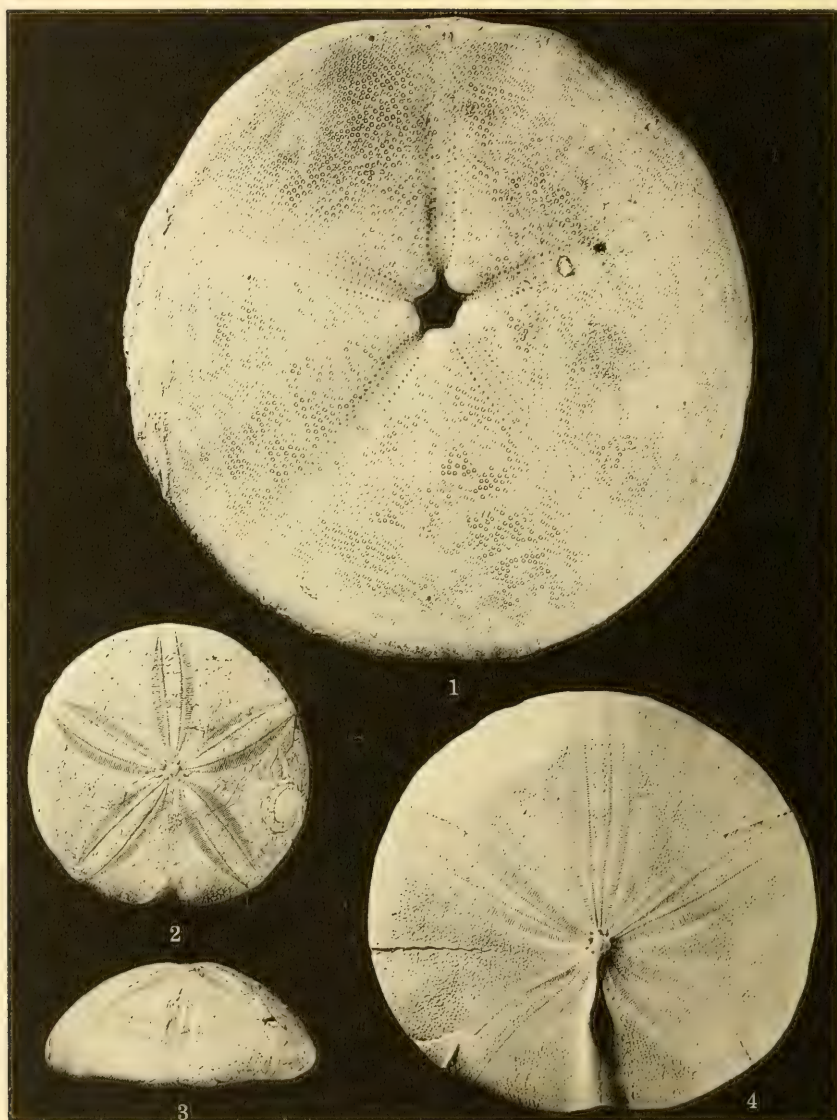




1, 2, *CLYPEUS SINUATUS* LESKE; 3-5, *CLYPEUS WYLLIEI* VAR.  
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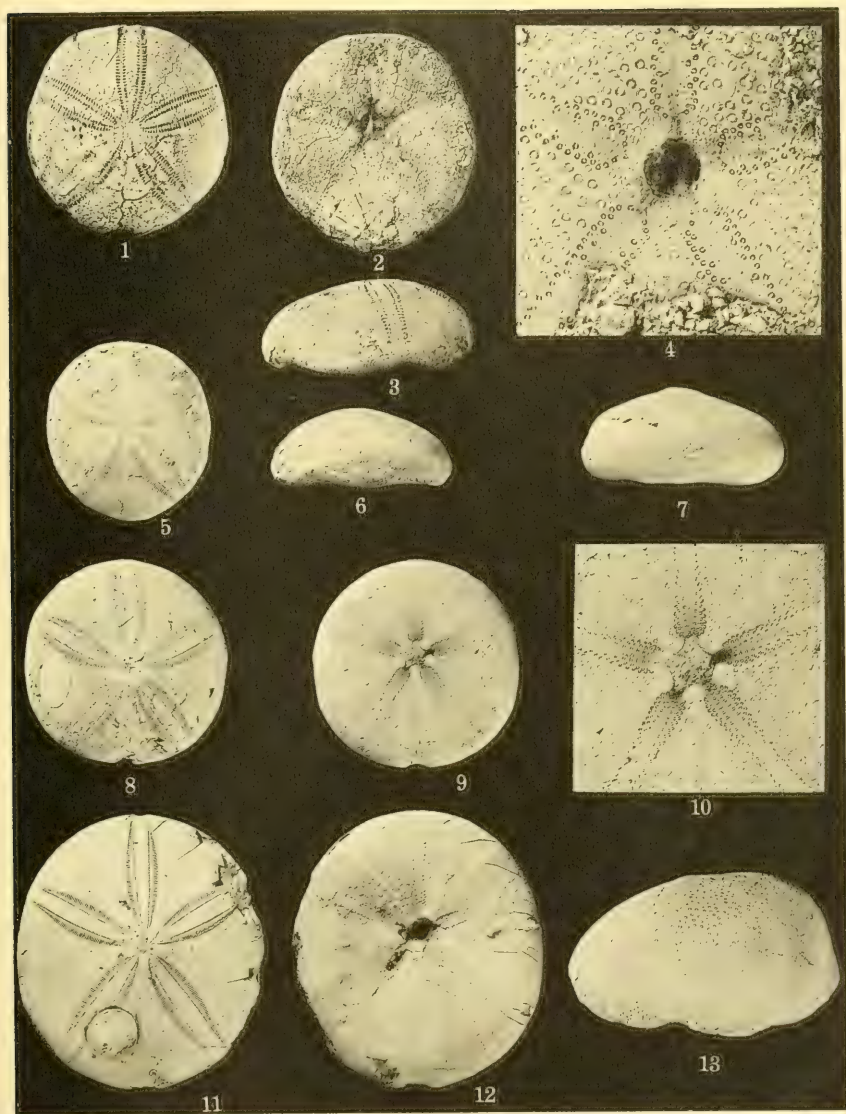
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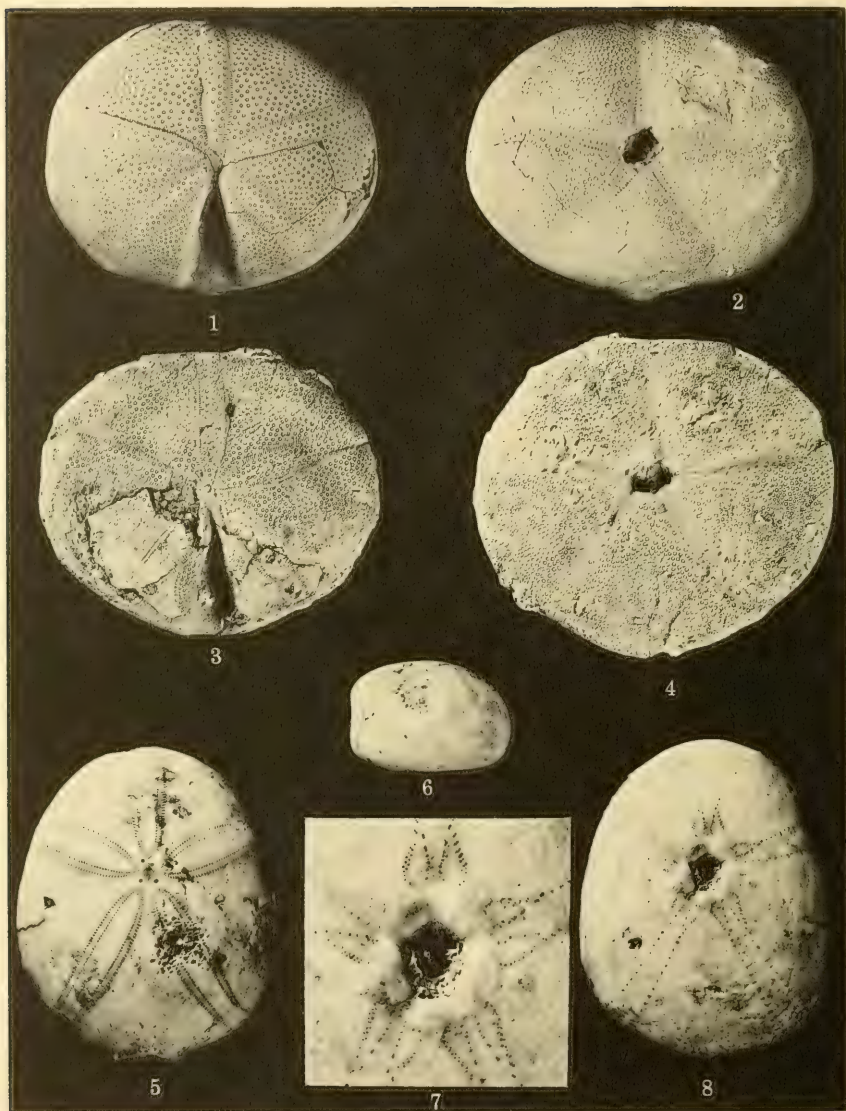
1, *CLYPEUS AGASSIZI* (WRIGHT); 2, 3, *CLYPEUS WYLLIEI* CURRIE;  
4, *CLYPEUS SINUATUS* LESKE

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1-4, *BOTHRYOPNEUSTES LAMBERTI* FOURTAU;  
5, 6, *BOTHRYOPNEUSTES LORIOLI* (FOURTAU); 7-10, *BOTHRYO-*  
*PNEUSTES SOMALIENSIS* (CURRIE); 11, 12, *BOTHRYOPNEUSTES*  
*ORIENTALIS* FOURTAU; 13, *PSEUDOSORELLA ORBIGNYANA* (COTTEAU)

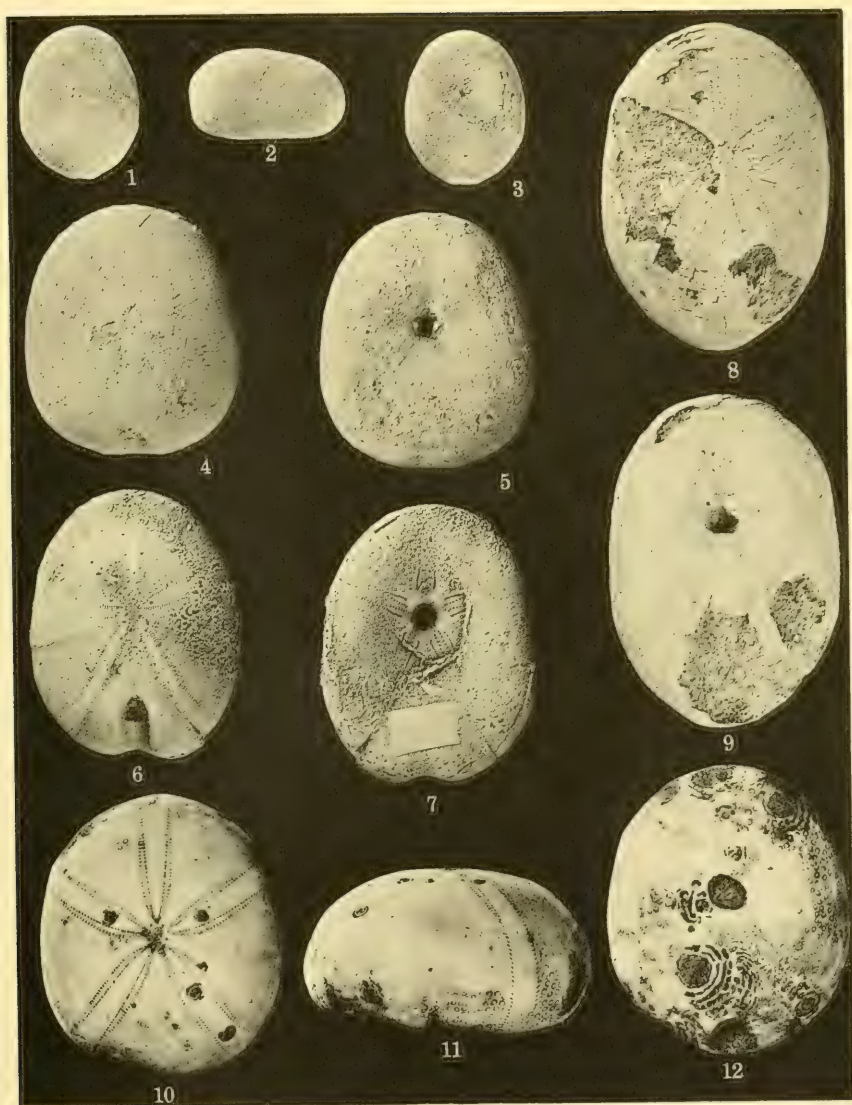
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1, 2, *PSEUDOSORELLA ORBIGNYANA* (COTTEAU);  
3, 4, *PSEUDOSORELLA SYRIACA* (DE LORIO); 5-8, *CATOPYGUS*  
*CARINATUS* (GOLDFUSS)

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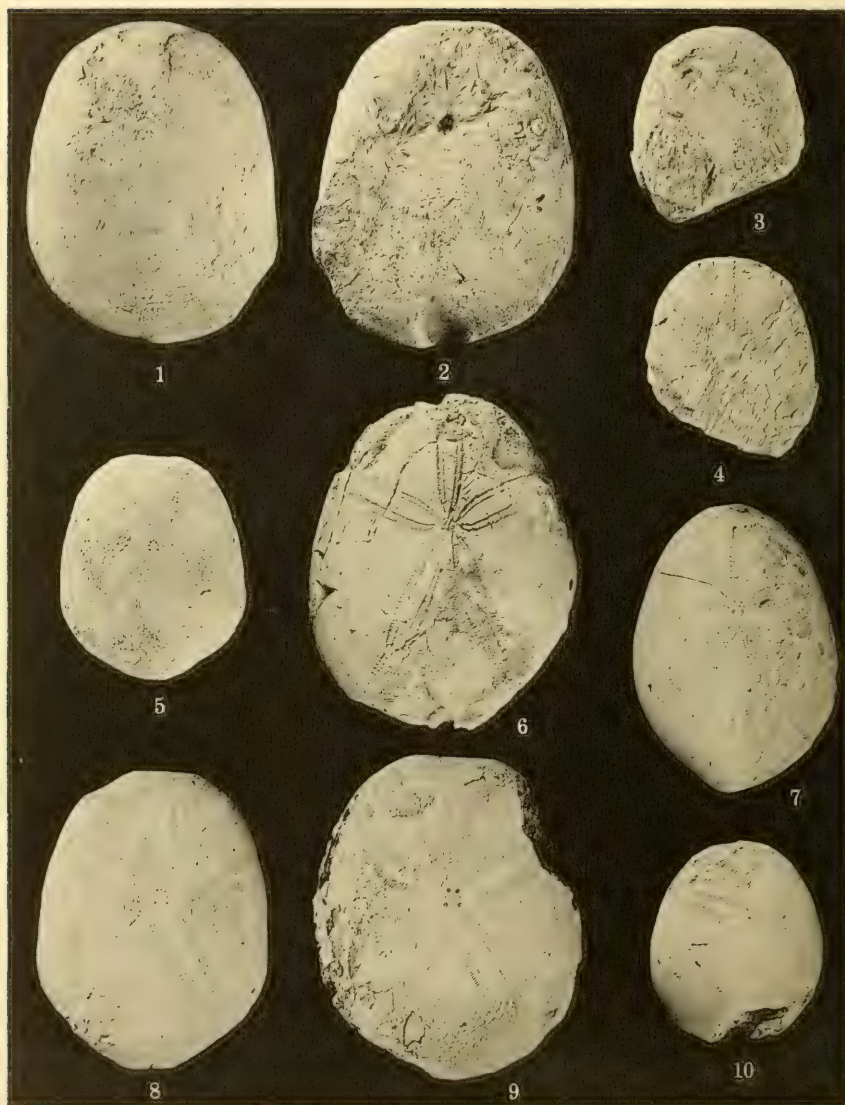




1-3 CATOPYGUS BARGESII (D'ORBIGNY); 4, 5, PHYLLOBRISUS  
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8, 9, PYGAULUS COUZENSIS DEMOLY AND LAMBERT;  
10-12, PYGAULUS DESMOULINSII AGASSIZ

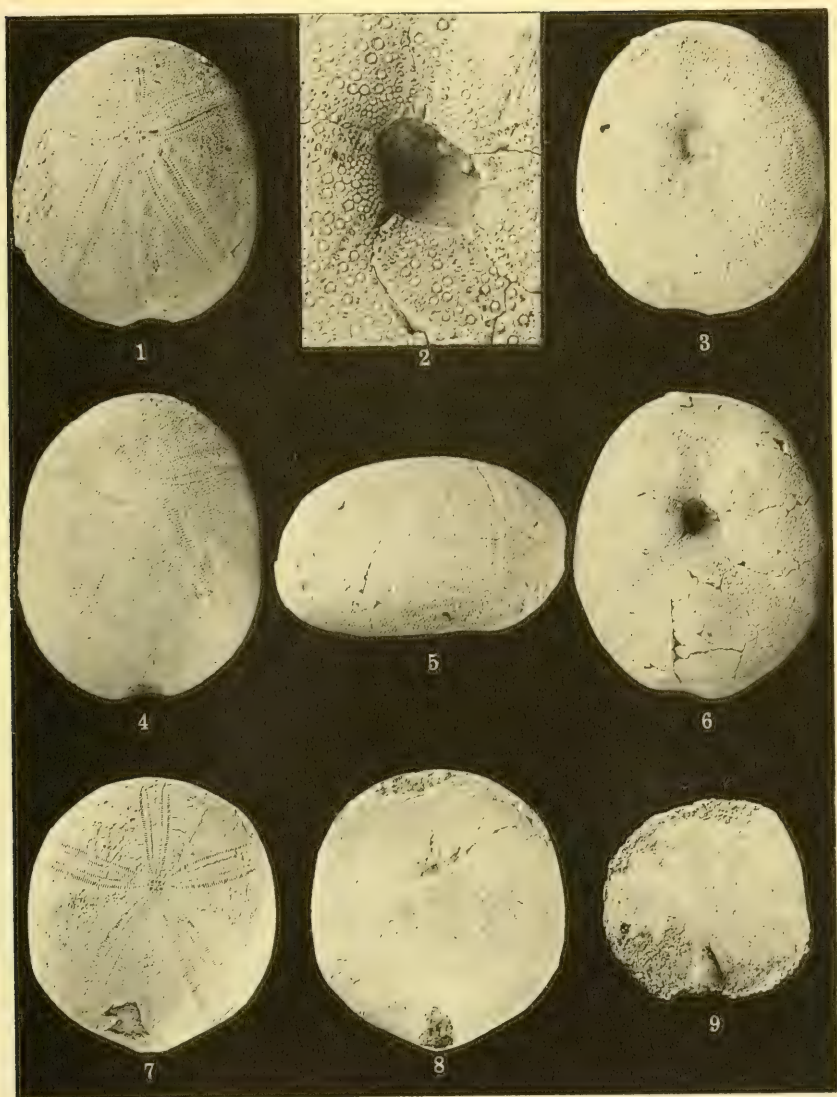
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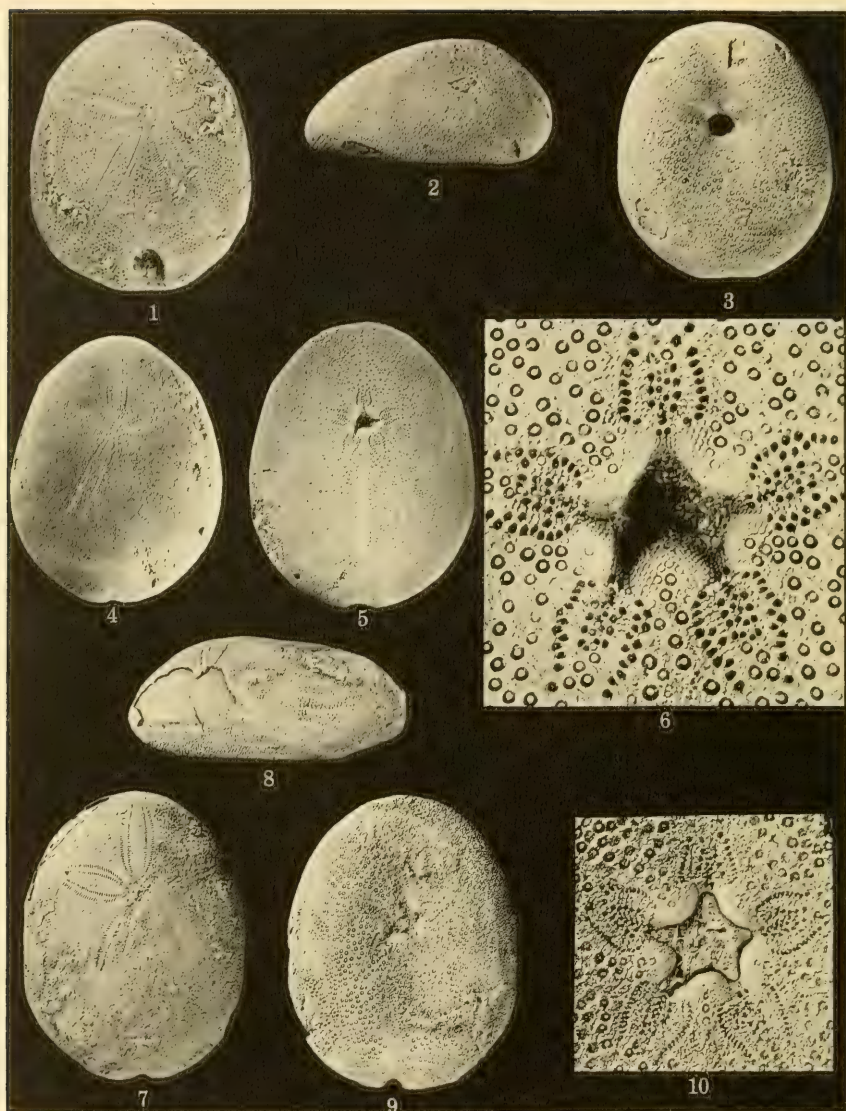
1-5, *Pygorhynchus obovatus* (Agassiz); 6, *Parapygus toucasanus* (D'Orbigny); 7, 8, *Pygorhynchus minor* (Agassiz); 9, 10, *Pygorhynchus cyclindricus* (Desor)

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-6, *PYGOPISTES COQUANDI* (COTTEAU); 7, 8, *HYPOPYGURUS GAUDRYI* GAUTHIER; 9, *CLYPEOPYGUS PAULTREI* (COTTEAU)

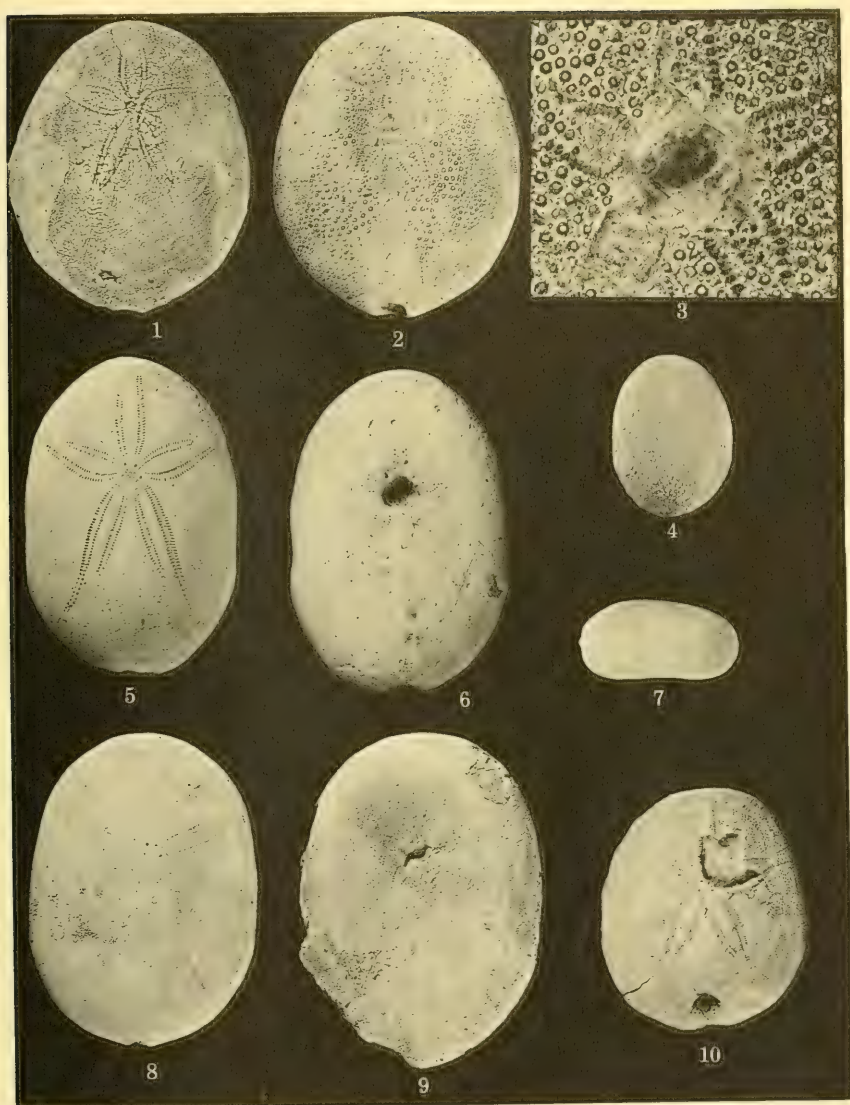
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1, 3, *PLAGIOCHASMA OLTERSII* (AGASSIZ); 4-6, *PARAPYGUS*  
*COTTEAUANUS* (D'ORBIGNY); 7-10, *PARAPYGUS* *CASSIDULOIDES*  
 GAUTHIER

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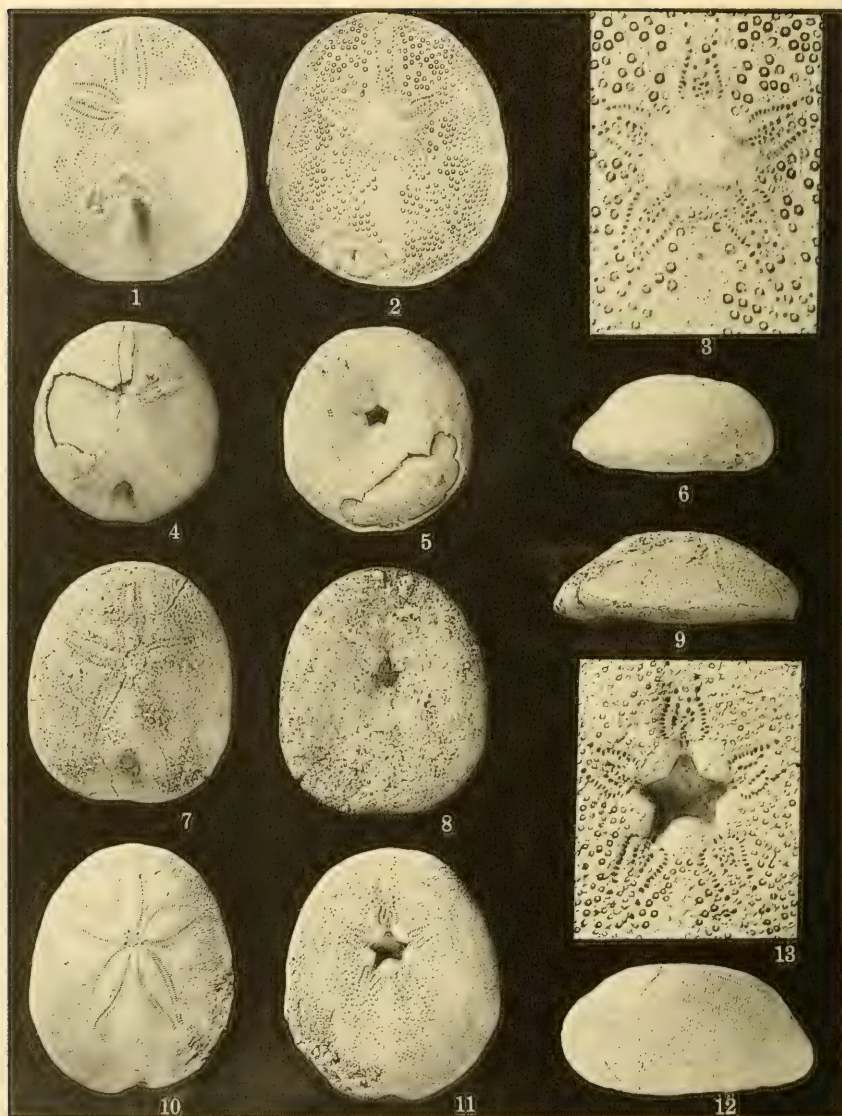




1, 2, *PARAPYGUS COQUANDI* (COTTEAU); 3, 4, *PARAPYGUS LONGIOR*  
(COTTEAU AND GAUTHIER); 5-7, *ARNAUDASTER GAUTHIERI* LAMBERT;  
8, 9, *PARAPYGUS NANCLASI* (COQUAND); 10, *PETALOBRISSUS*  
*TRIGONOPYGUS* (COTTEAU)

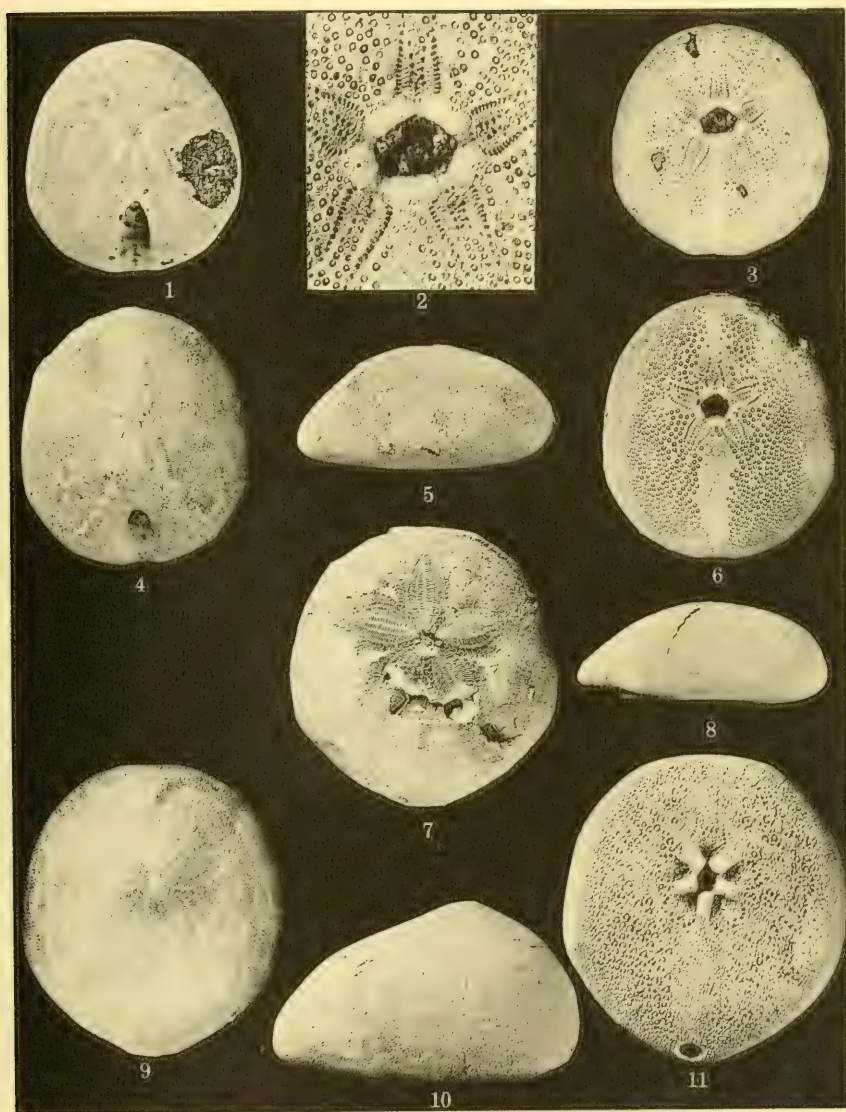
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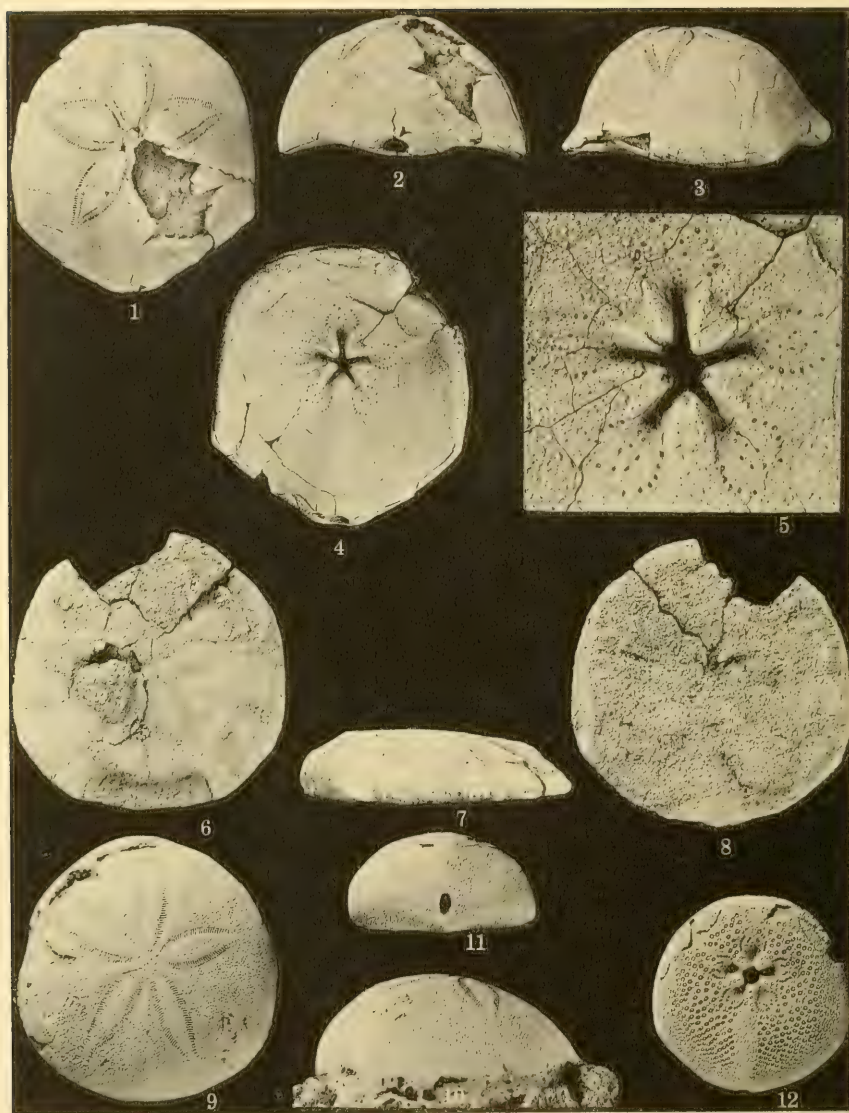
1-3, *PETALOBRISSUS DJELFENSIS* (GAUTHIER); 4-6, *PETALOBRISSUS*  
*LEFEBVREI* (FOURTAU); 7-9, *PETALOBRISSUS AMMONIS* (FOURTAU);  
 10-13, *PETALOBRISSUS SETIFENSIS* (COTTEAU)

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1-3, PETALOBRISSUS NELTNERI (LAMBERT); 4-6, PETALOBRISSUS  
CUBENSIS (WEISBORD); 7, 8, EURYPETALUM FAUJASIIUM  
(DESMOULINS); 9-11, FAUJASIA APICALIS (DESOR)

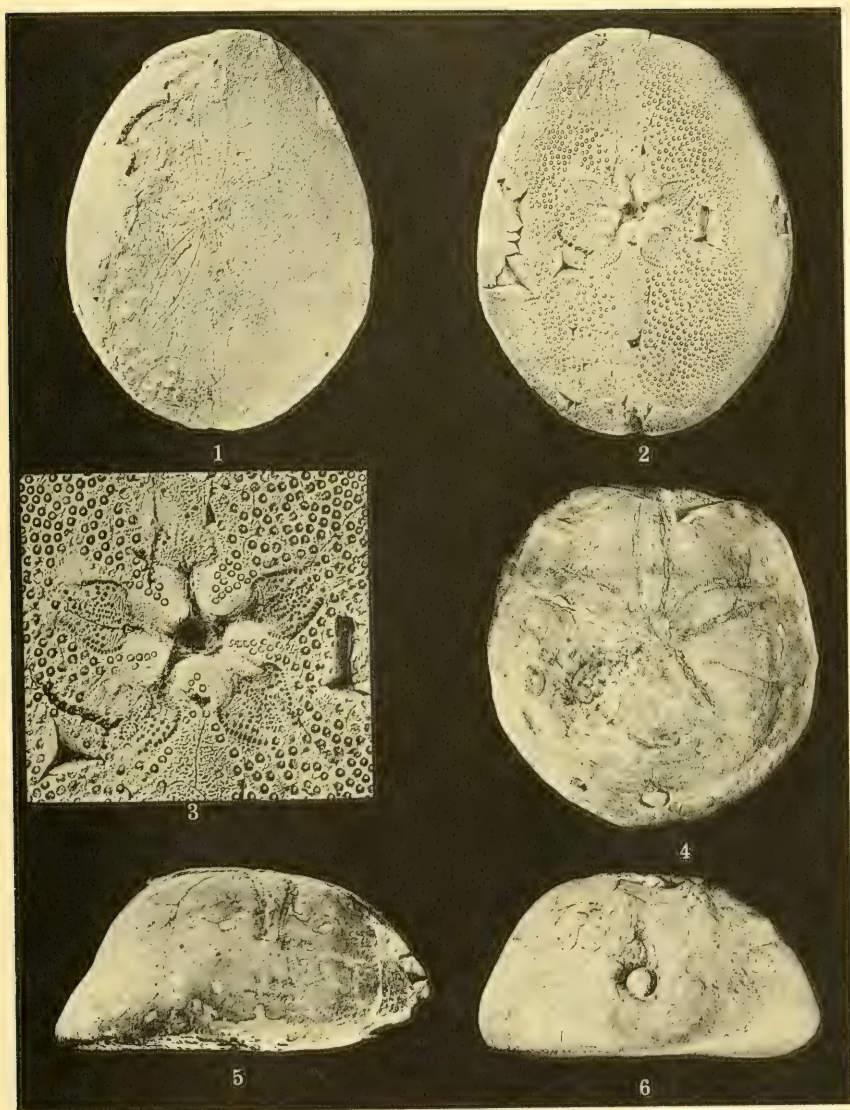
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1-5, *DOMECHINUS CHELONIUM* (COOKE); 6-8, *FAURASTER PRISCUS* LAMBERT; 9-12, *LEFORTIA DELGADOI* (DE LORIO)

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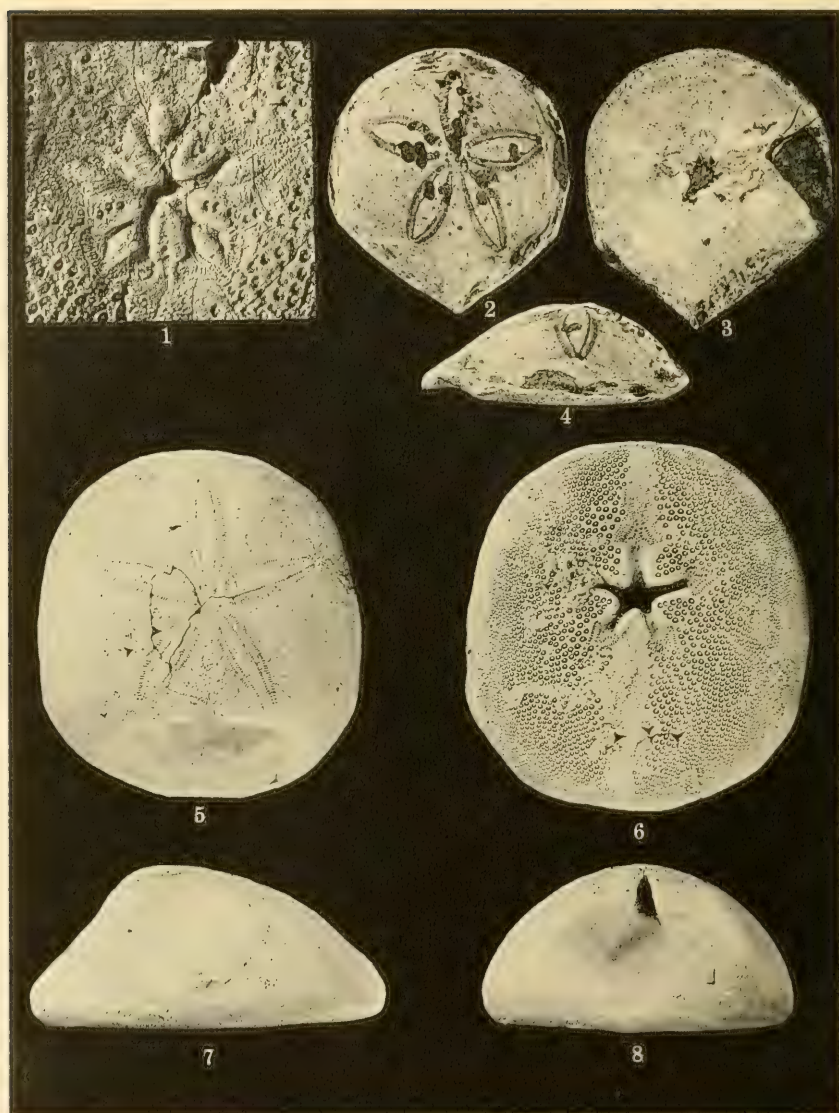




1-3, *Pygurostoma morgani* COTTEAU AND GAUTHIER;  
4-6, *Gongrochanus herschelanus* (M'CLELLAND)

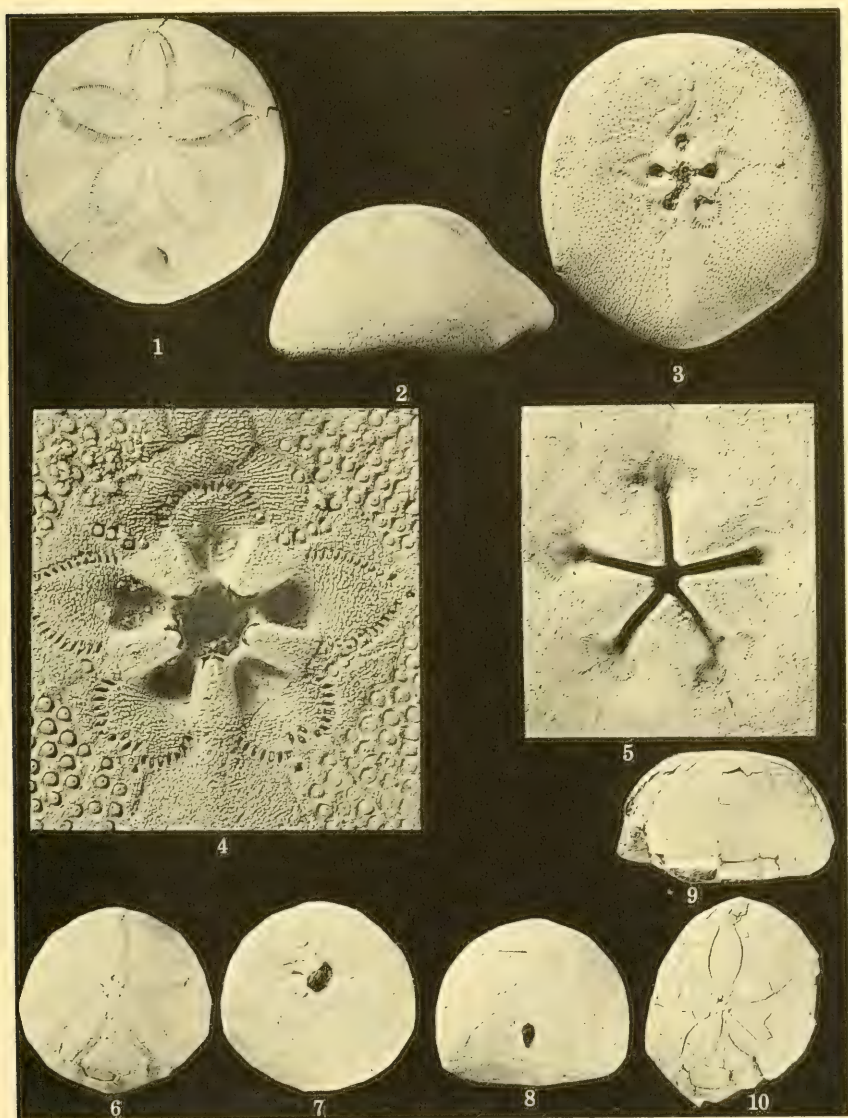
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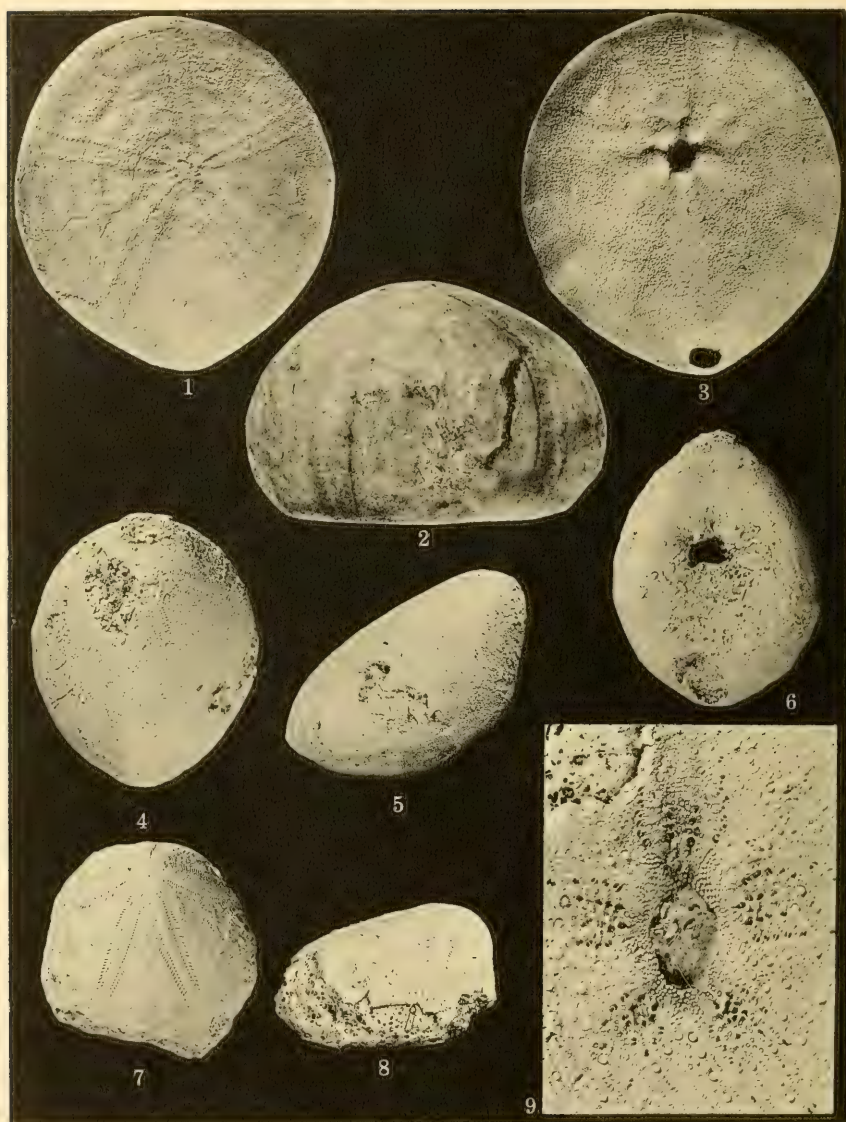
1, *GONGROCHANUS HERSCHELIANUS* (M'CLELLAND);  
2-4, *PYGIDIOLAMPAS EURYNOTA* CLARK; 5-8, *STIGMATOPYGUS*  
*LAMBERTI* BESAIRIE

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1-4, *HARDOUINIA MORTONIS* (MICHELIN); 5, *HARDOUINIA PORRECTUS* (CLARK); 6-10, *HARDOUINIA HEMISPHERICA* (SLOCUM)

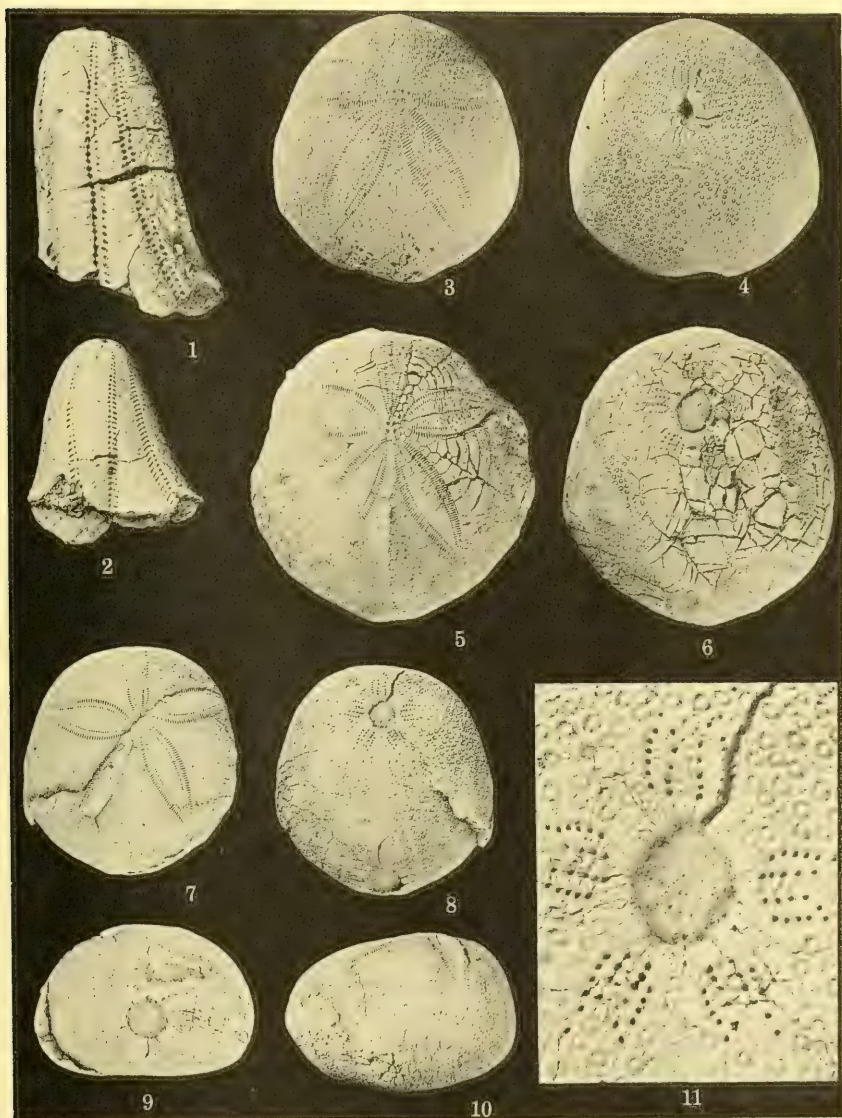
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1-3, *HEMICARA POMERANUM* SCHLUTER; 4-6, *ARCHIACIA SANDALINA* AGASSIZ; 7-9, *ARCHIACIA PALMATA* GAUTHIER

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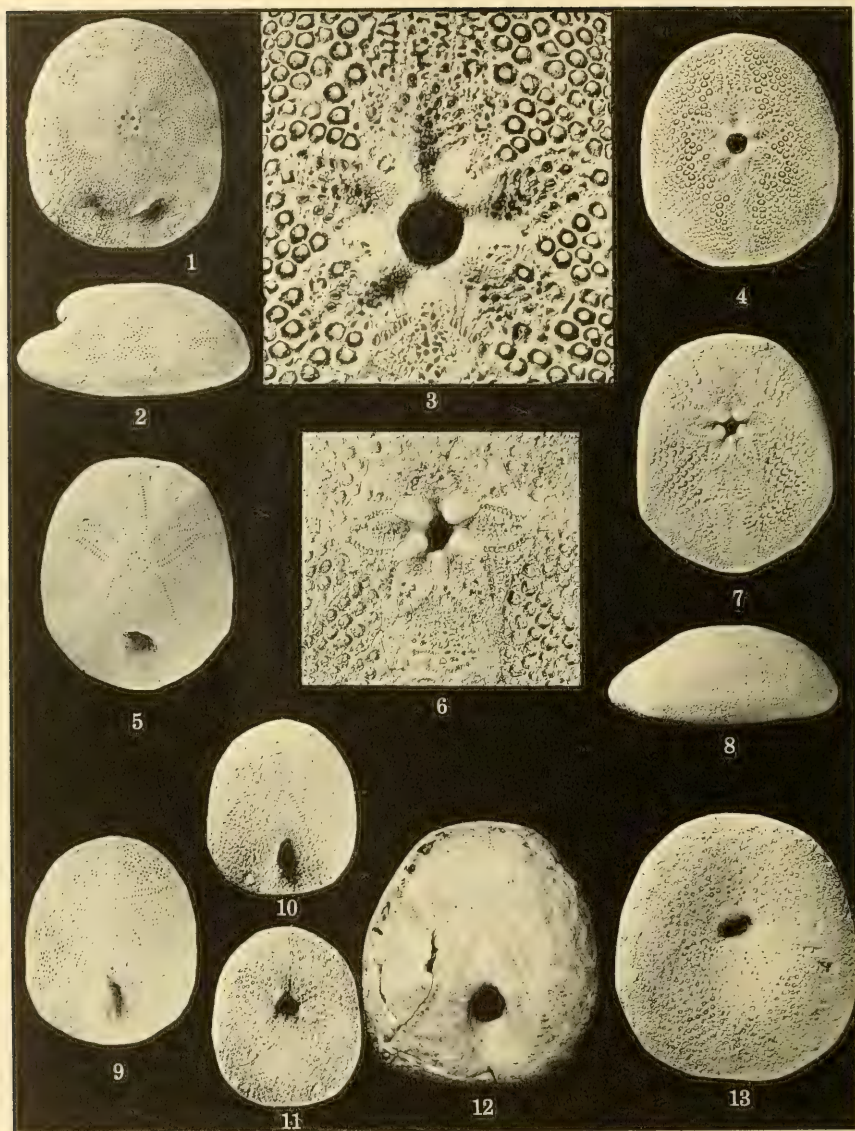




1, *CLAVIASTER CORNUTUS* (AGASSIZ); 2, *CLAVIASTER LIBYCUS* GAUTHIER; 3, 4, *GENTILIA TAFILELTENSIS* ? LAMBERT; 5-11, *GENTILIA SYRIENSIS* KIER

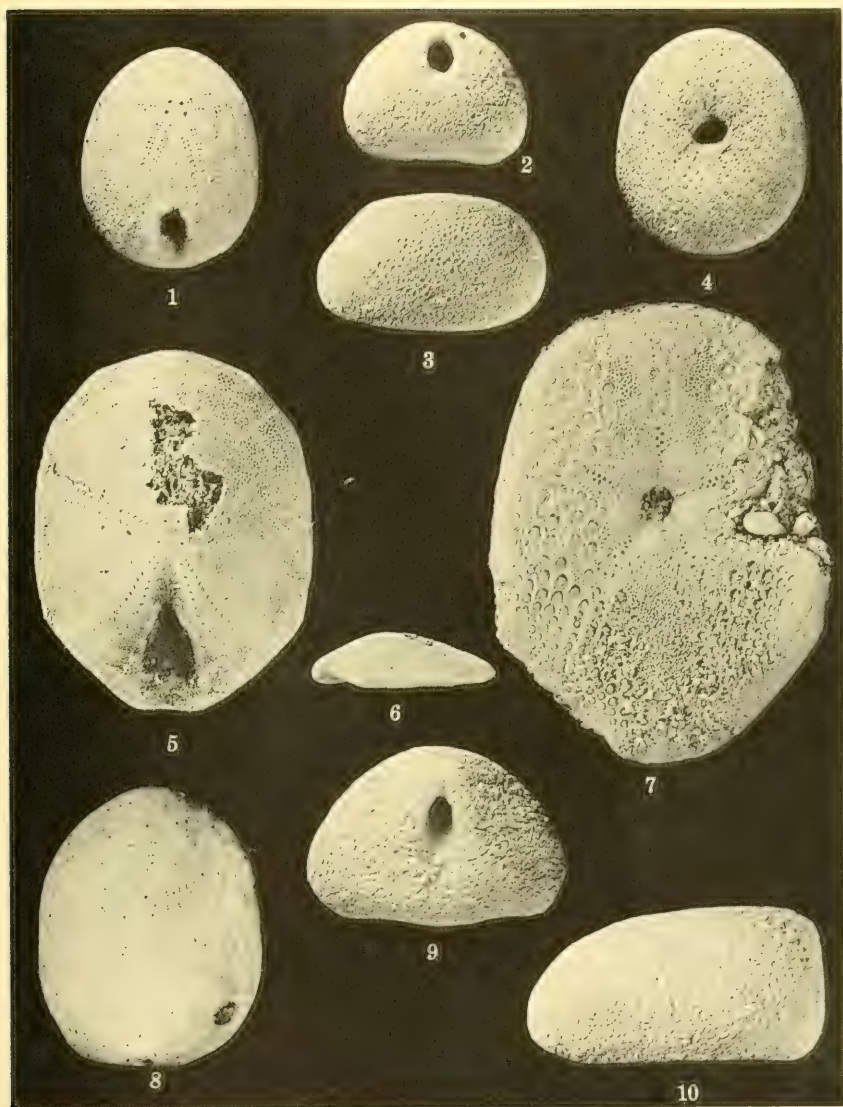
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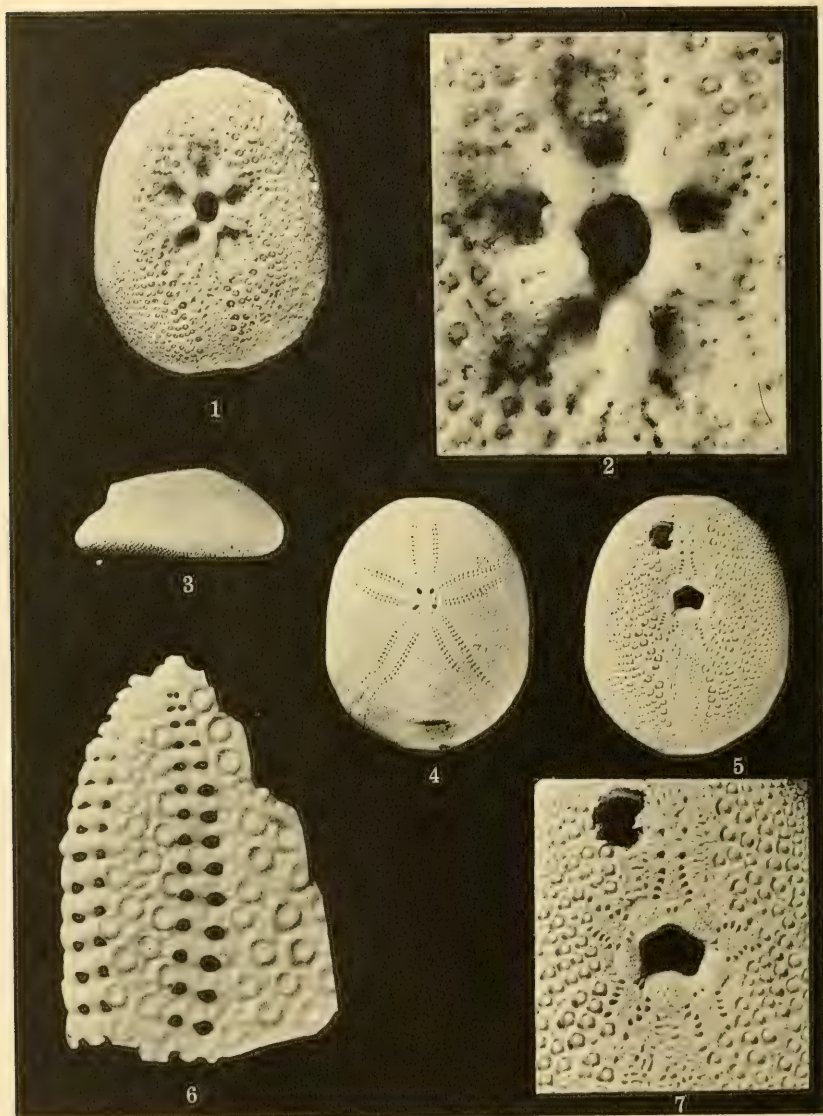
1-4, *RYNCHOPYGUS MARMENI* (AGASSIZ); 5-8, *RYNCHOPYGUS LAPISCANCRI* (LESKE); 9, *NUCLEOPYGUS SIMILIS* (D'ORBIGNY); 10, 11, *NUCLEOPYGUS MINOR* DESOR; 12, 13, *NUCLEOPYGUS ANGUSTATUS* (CLARK)

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1-4, *NUCLEOPYGUS SCROBICULATUS* (GOLDFUSS); 5-7, *OCHETES MORRISII* (FORBES); 8-10, *HYSOPYGASTER UNGOSENSIS* BAJARUNAS

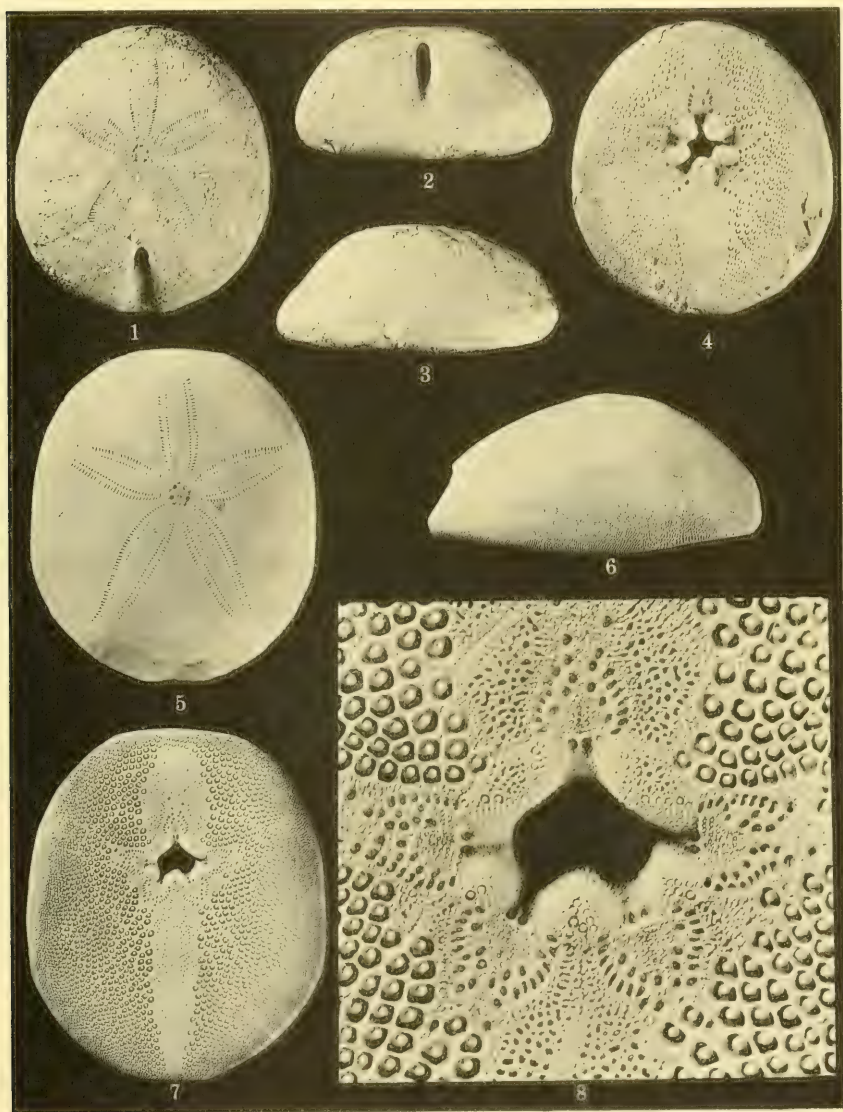
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1, 2, *HYPSOPYGASTER UNGOSENSIS* BAJARUNAS; 3-7, *CASSIDULUS CARIBOEARUM* LAMARCK

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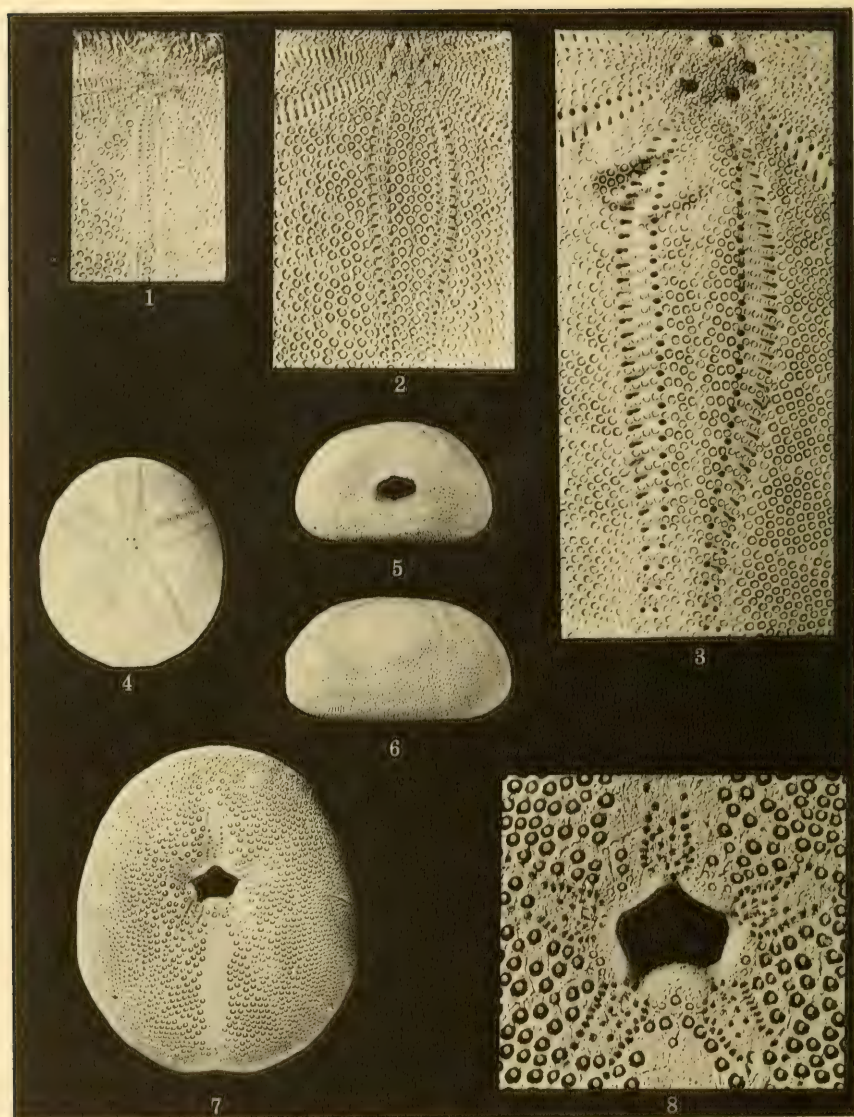




1-4, *AUSTRALANTHUS LONGIANUS* (GREGORY);  
5-8, *RHYNCHOLAMPAS PACIFICUS* (A. AGASSIZ)

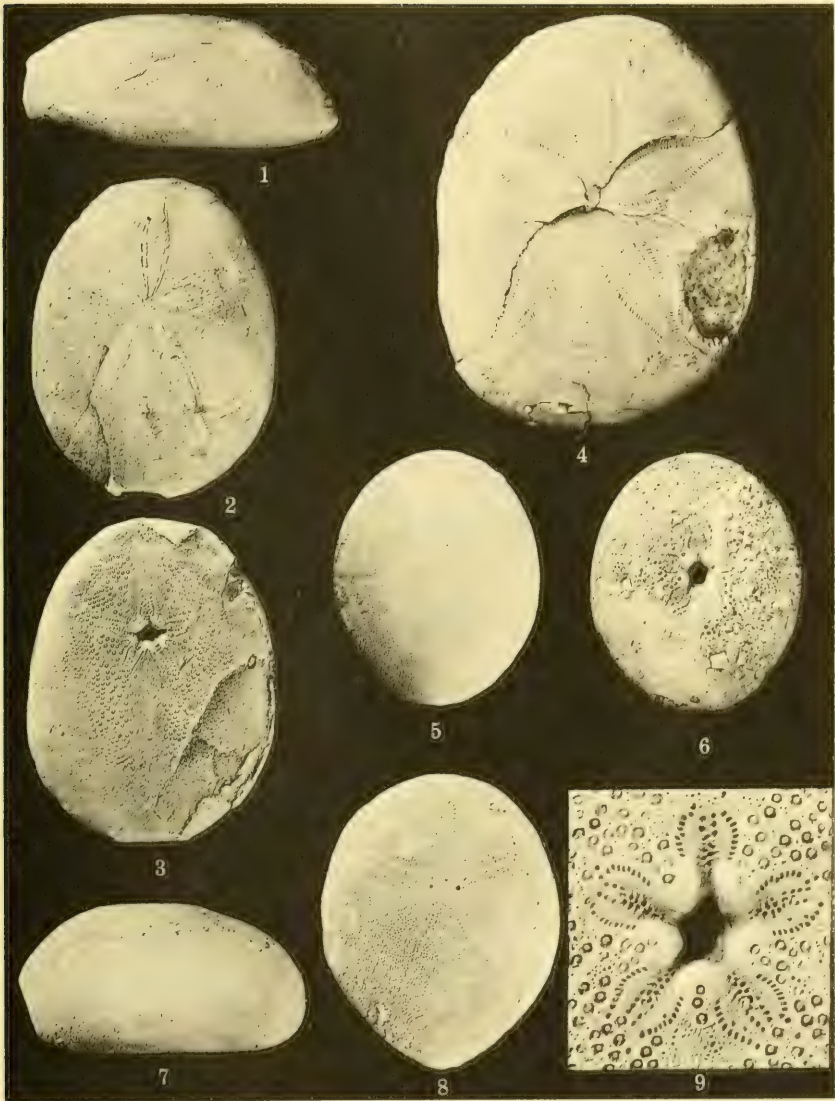
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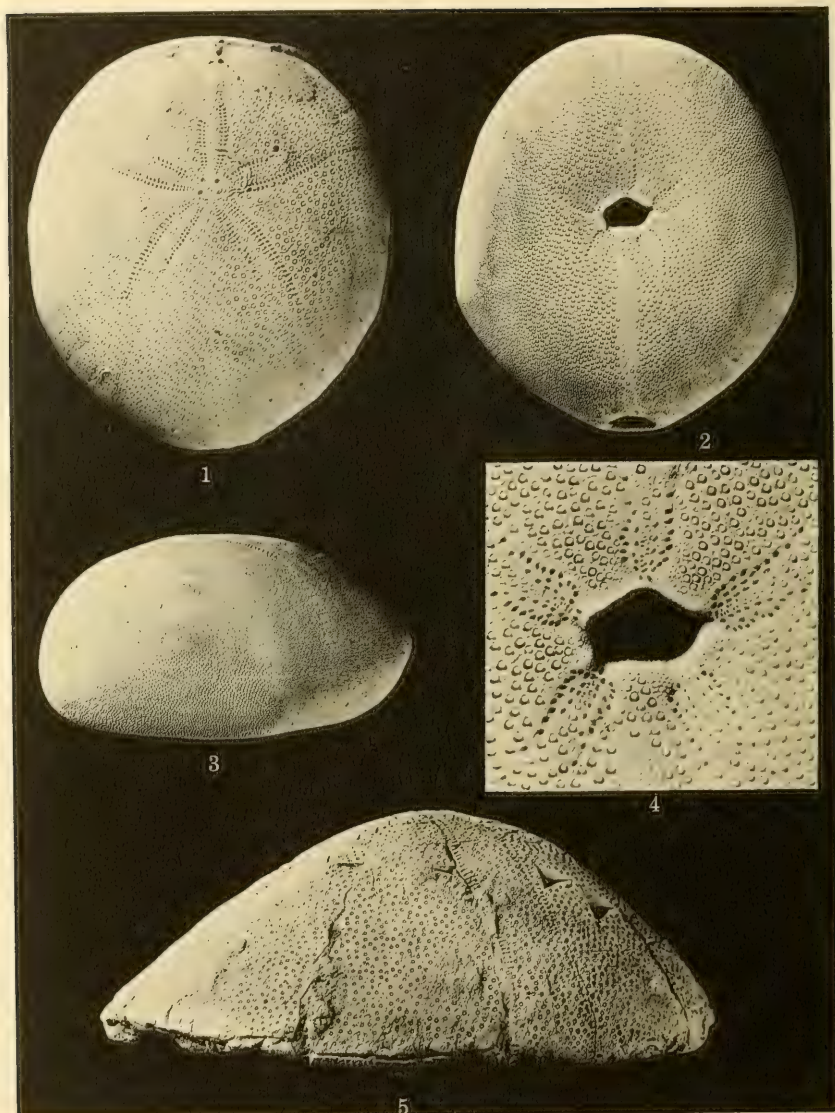
1-3, *RHYNCHOLAMPAS PACIFICUS* (A. AGASSIZ);  
4-8, *RHYNCHOLAMPAS GRIGNONENSIS* (DEFRANCE)

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-3, *RYNCHOLAMPAS ELLIPTICUS* (ARNOLD AND CLARK);  
4, *RYNCHOLAMPAS MEXICANUS* (KEW); 5, 6, *OOLOPYGUS*  
*GRACILIS* LAMBERT; 7-9, *OOLOPYGUS PYRIFORMIS* (LESKE)

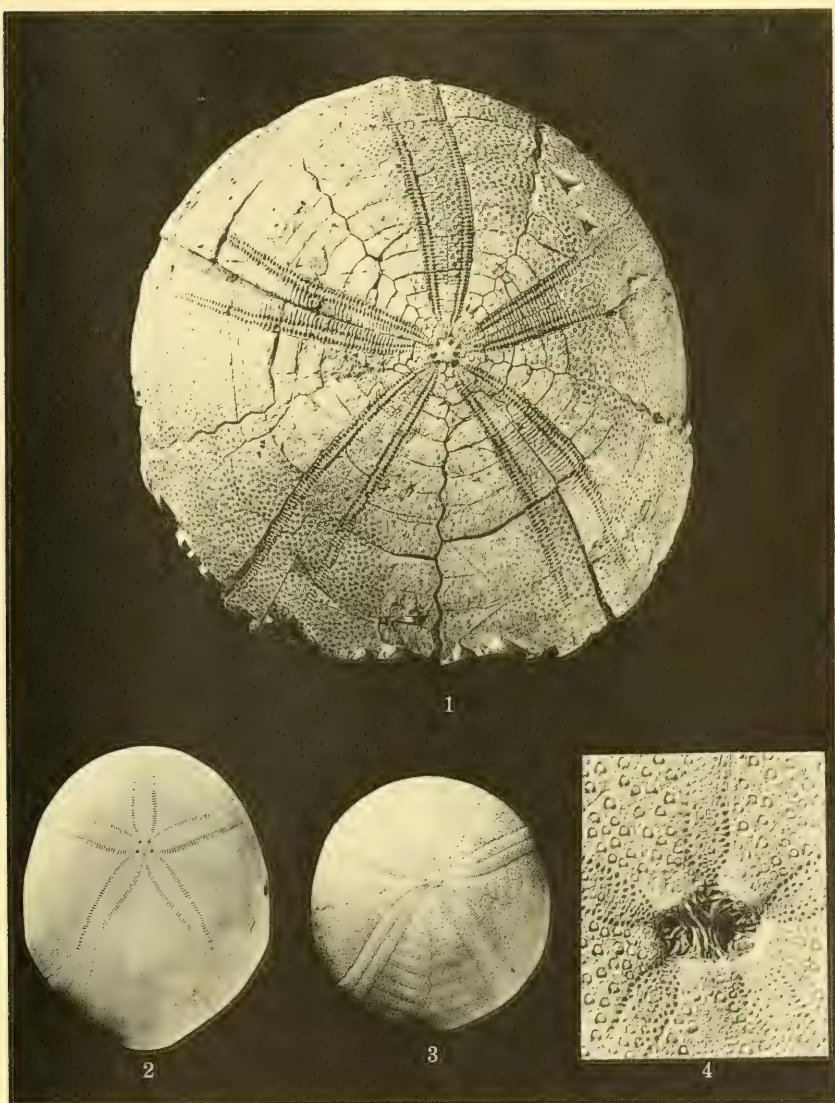
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1-4, *ECHINOLAMPAS OVIFORMIS* (GMELIN); 5, *ECHINOLAMPAS*  
*LUCAE* (DESOR)

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1, *ECHINOLAMPAS LUCAE* (DESOR); 2, *ECHINOLAMPAS DEPRESSA* GRAY; 3, 4, *ECHINOLAMPAS CRASSA* (BELL)

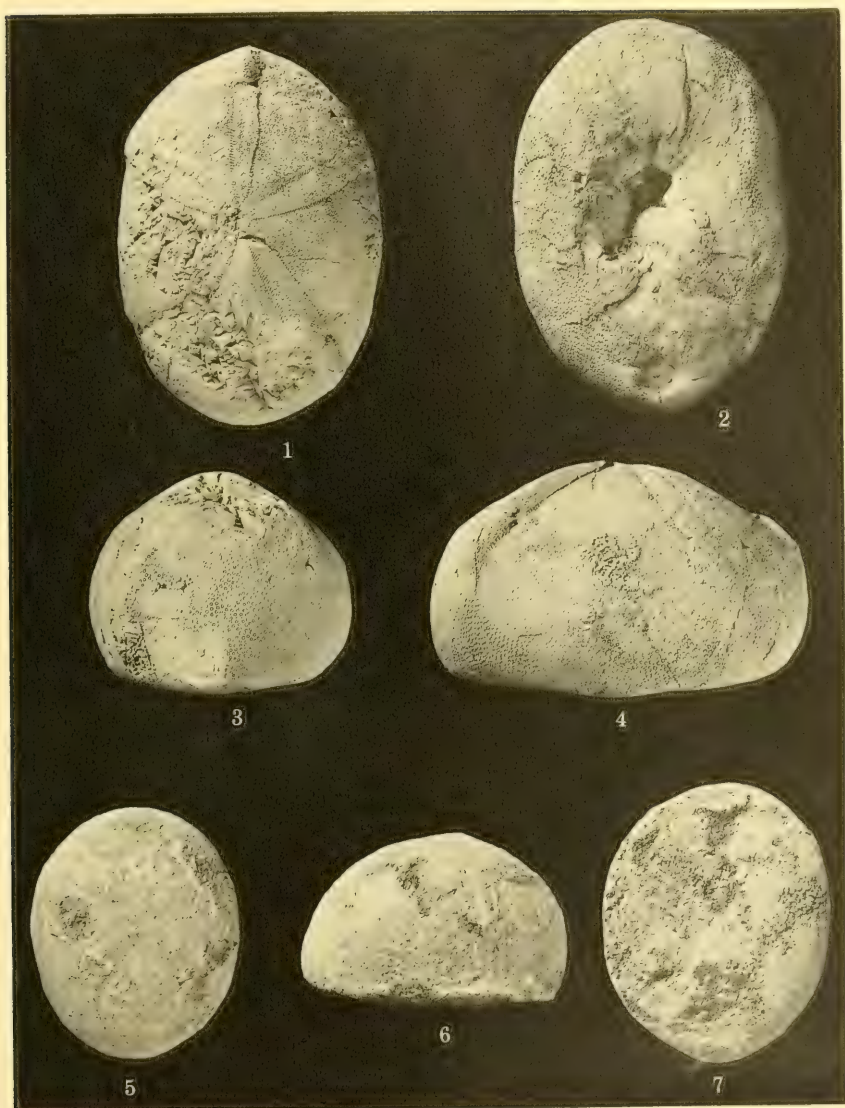
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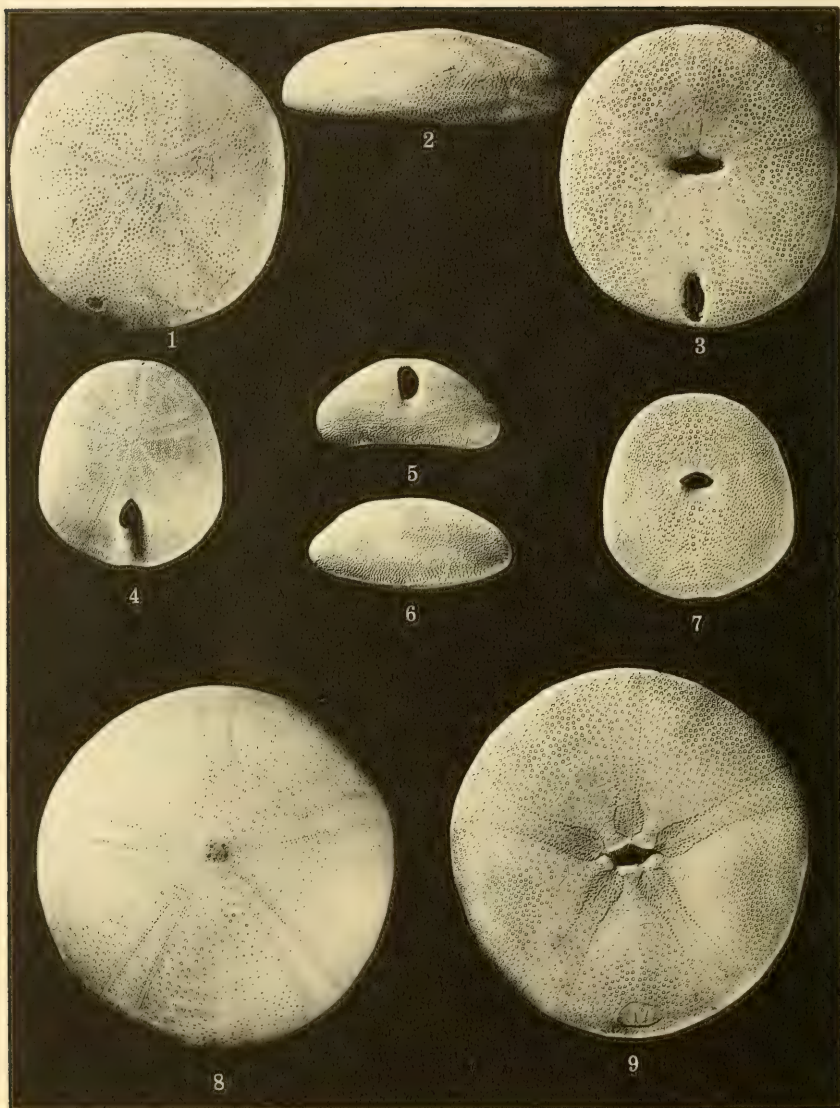
1, *ECHINOLAMPAS LUCAE* (DESOR); 2-4, *ECHINOLAMPAS LEHONI* (COTTEAU); 5-7, *ECHINOLAMPAS POSTEROCRASSUS* GREGORY

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-4, *ECHINOLAMPAS RAULINI* COTTEAU; 5-7, *VOLOGESIA*  
*HUNGARICA* (SZÖRENYI)

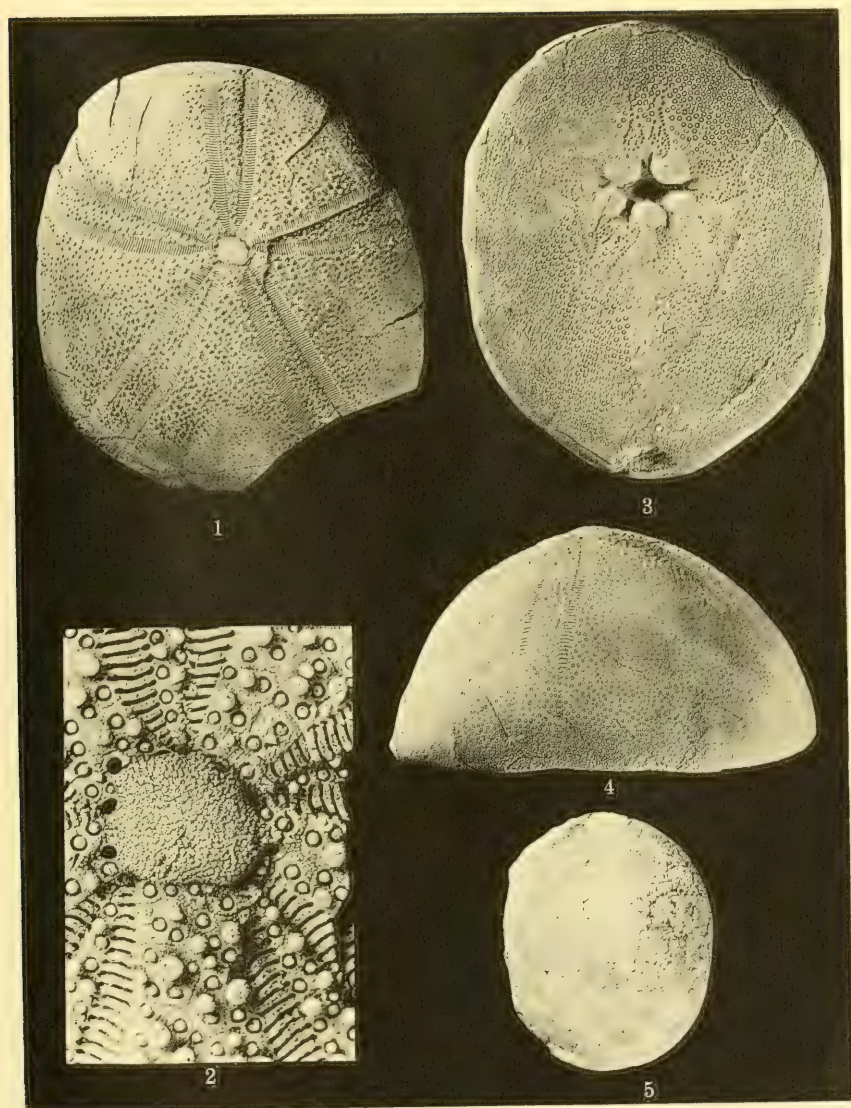
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1-3, *Plesiolampas placenta* DUNCAN AND SLADEN;  
4-7, *Apatopygus recens* (MILNE EDWARDS); 8, 9, *Conolampas*  
*sigsbei* (A. AGASSIZ)

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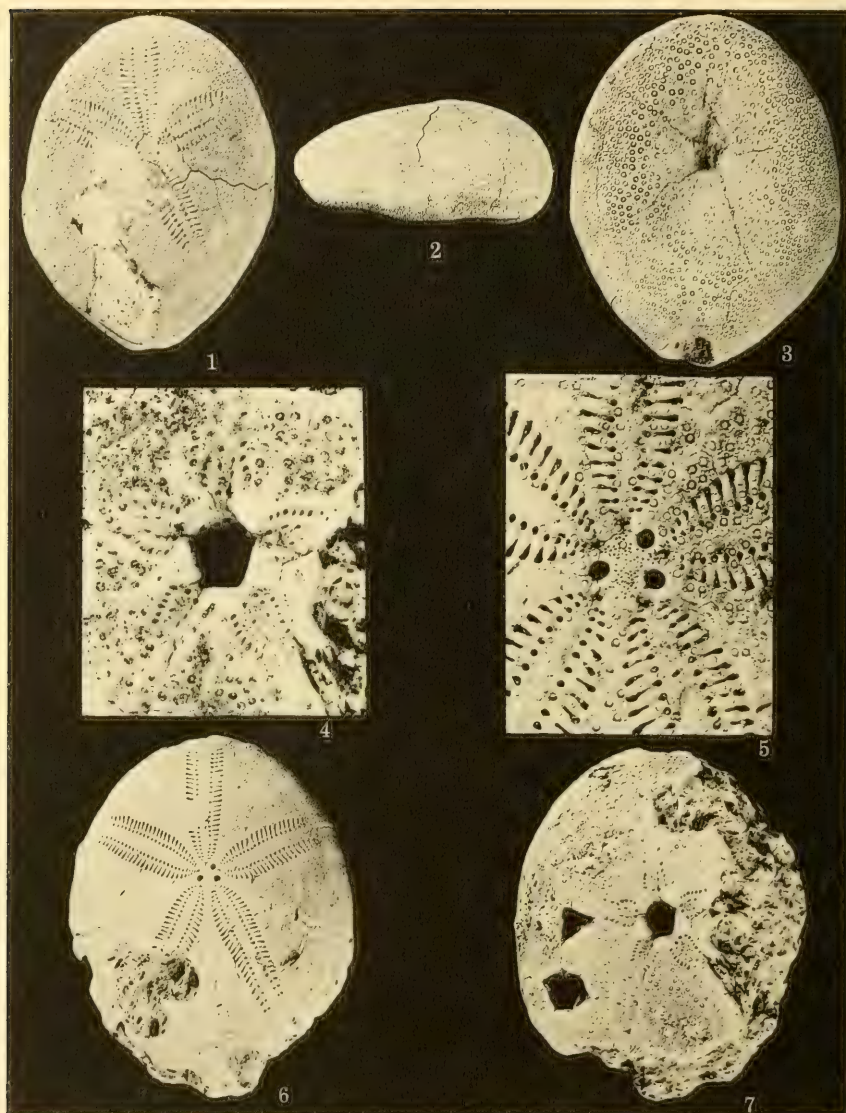




1-4, CLYPEOLAMPAS OVATUS (LAMARCK); 5, VOLOGESIA  
OVUM (GRATTELOUP)

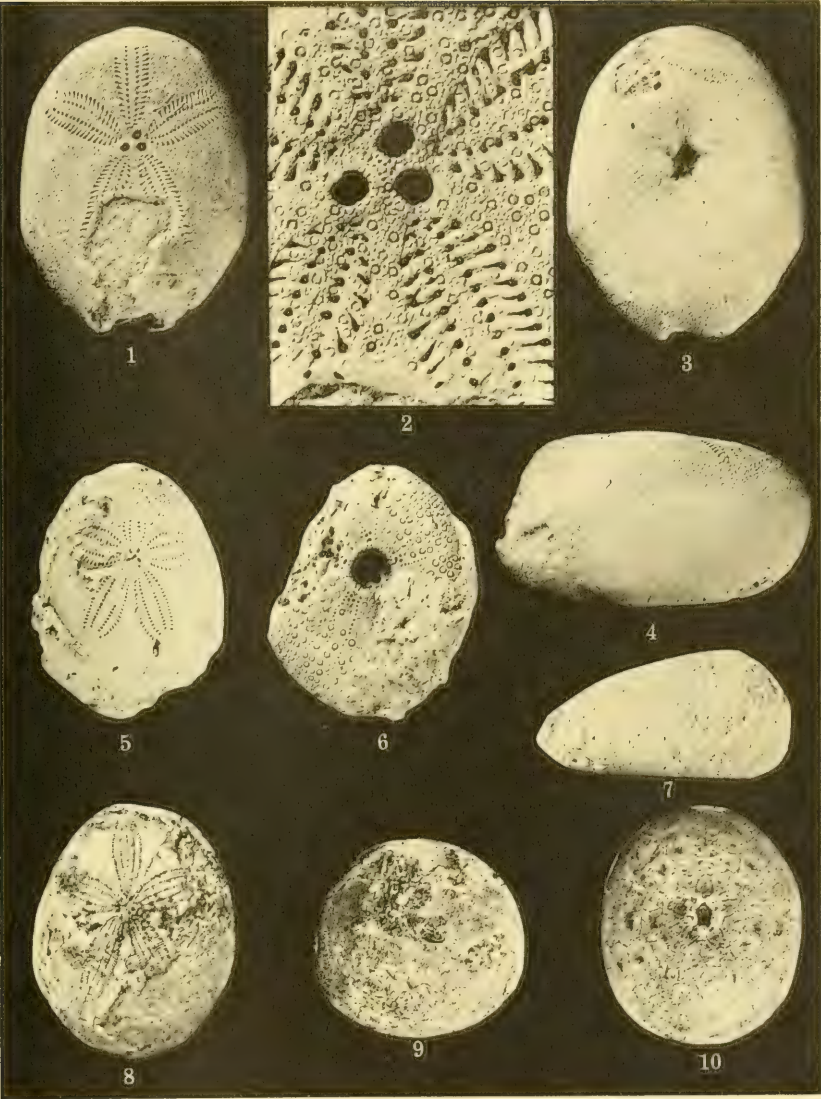
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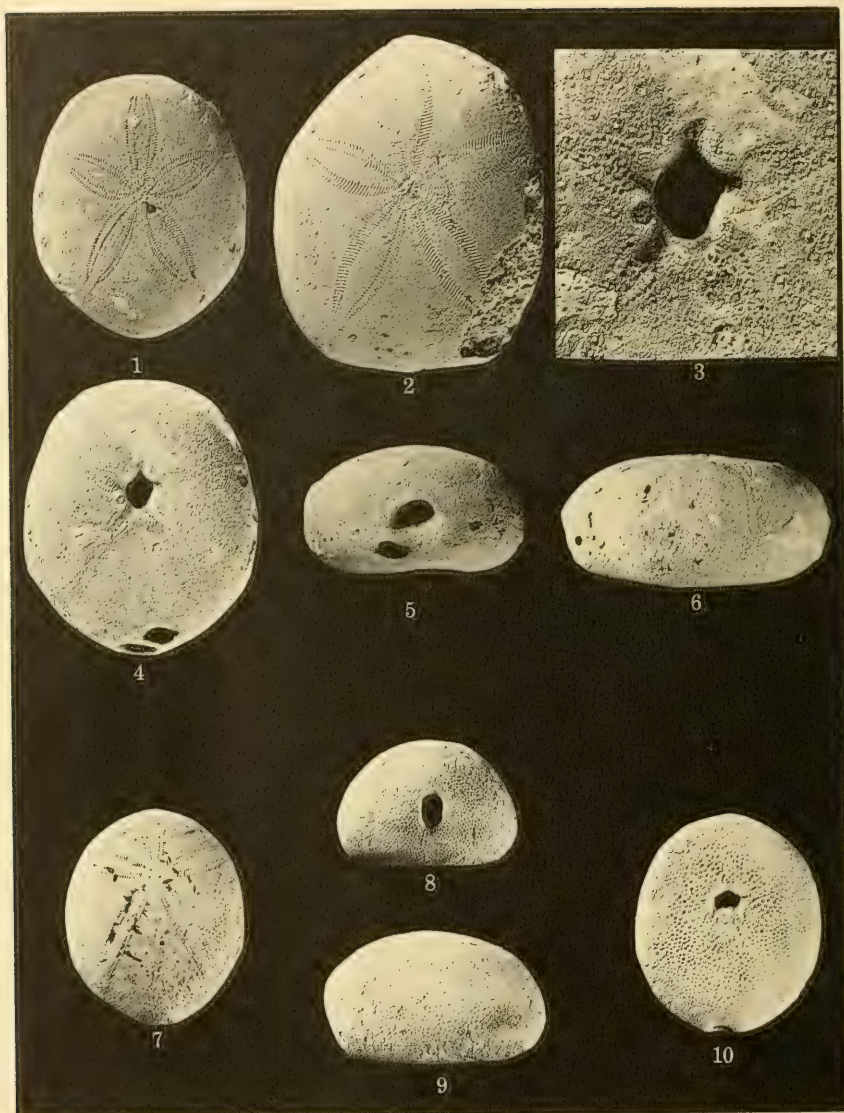
1-3, *PLIOLAMPAS GAUTHIERI* (COTTEAU); 4-7, *PLIOLAMPAS*  
*PIOTI GAUTHIER*

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-4, *PLIOLAMPAS VASSALLI* (WRIGHT); 5-7, *TERMIERIA HENRICI* LAMBERT; 8-10 *ZUFFARDIA SANFILIPPOI* (CHECCHIA-RISPOLI)

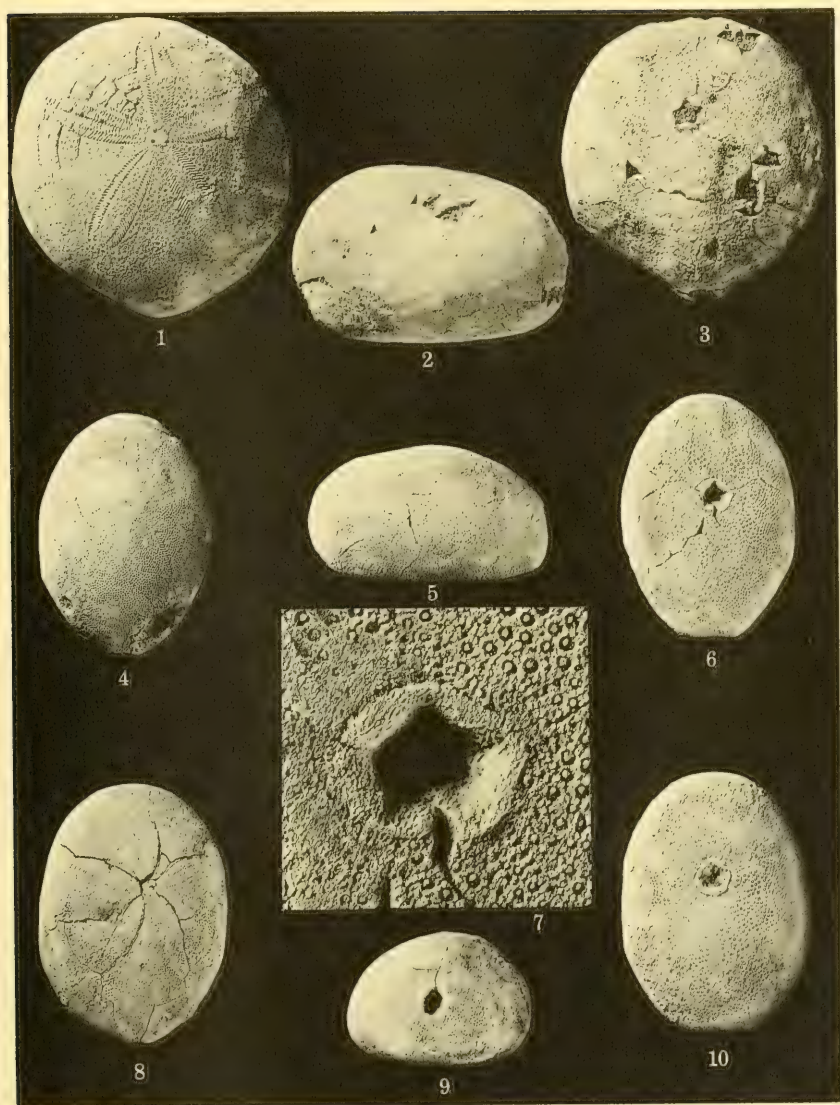
(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-6, *KEPHRENIA LORIOLI* FOURTAU; 7-10, *SANTEELAMPAS OVIFORMIS* (CONRAD)

(SEE EXPLANATION OF PLATES AT END OF TEXT.)





1-3, *NEOCATOPYGUS ROTUNDUS* DUNCAN AND SLADEN;  
4-10, *ILARIONIA BEGGIATOI* (LAUBE)

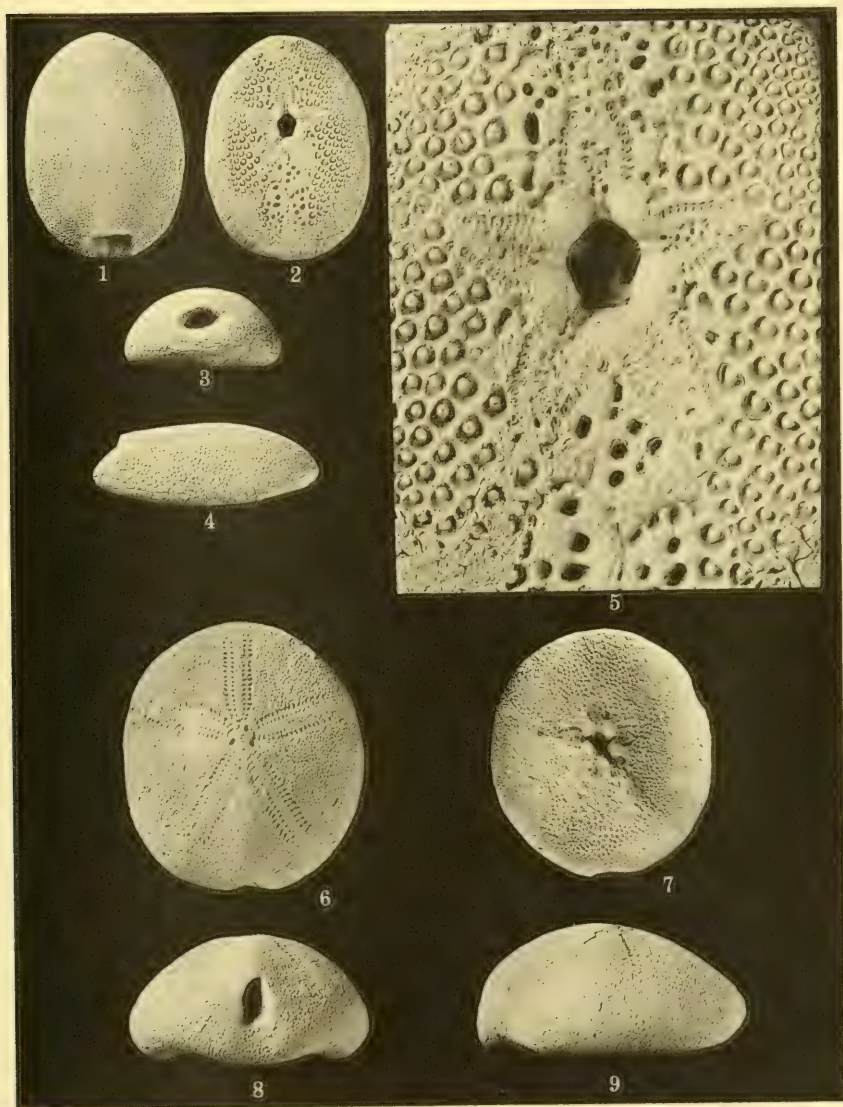
(SEE EXPLANATION OF PLATES AT END OF TEXT.)





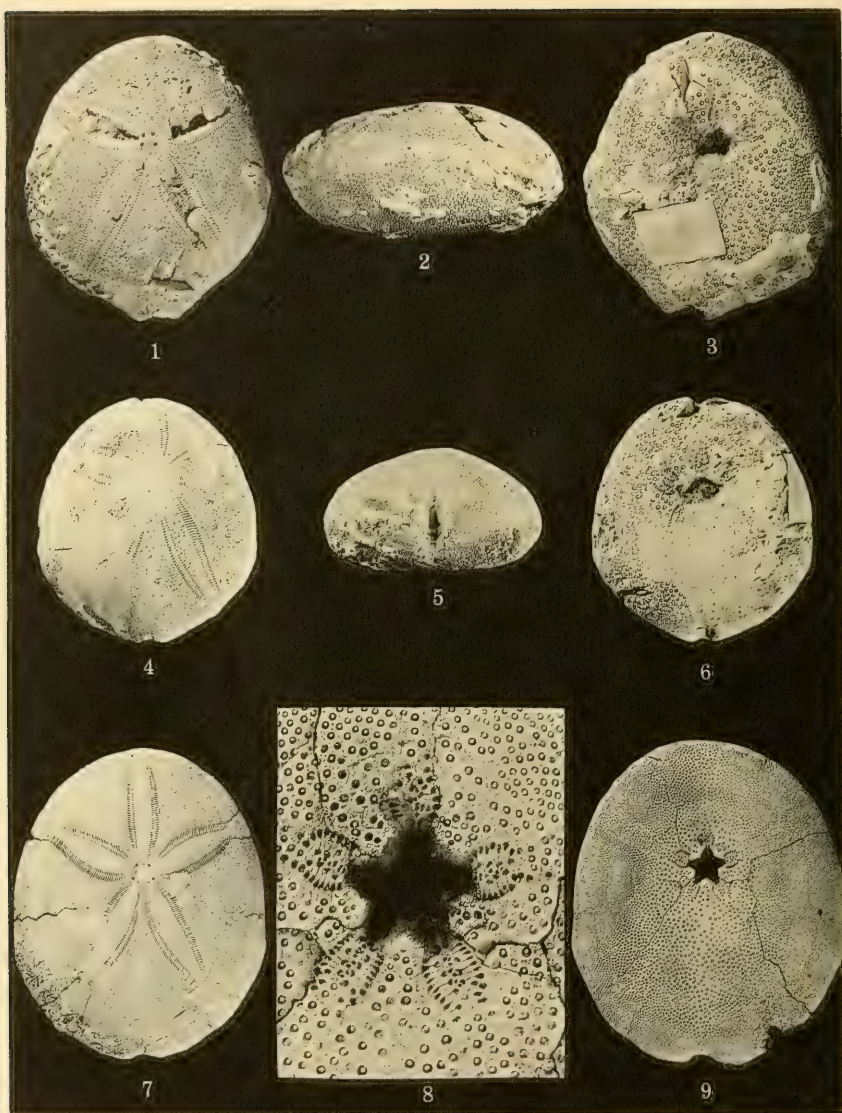
1, 2, *GITOLAMPAS CUVIERI* (MÜNSTER); 3-5, *GITOLAMPAS GEORGIENSIS* (TWITCHELL); 6-9, *EURHODIA MORRISI* HAIME

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-5, *EURHODIA RUGOSA* (RAVENEL); 6-9, *STUDERIA SUBCARINATUS* (GOLDFUSS)

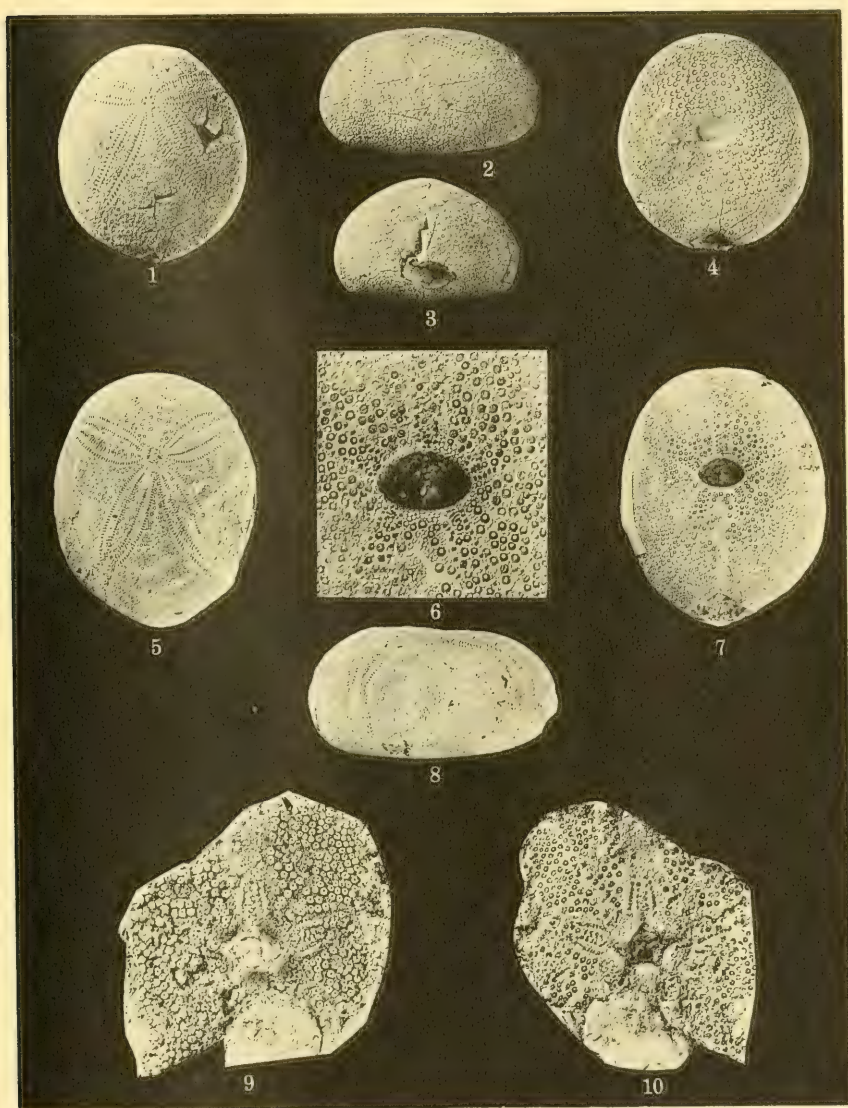
(SEE EXPLANATION OF PLATES AT END OF TEXT.)



1-6, GITOLAMPAS TUNETANA (GAUTHIER); 7-9, GITOLAMPAS  
ISSYAVIENSIS (MUNIER-CHALMAS)

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

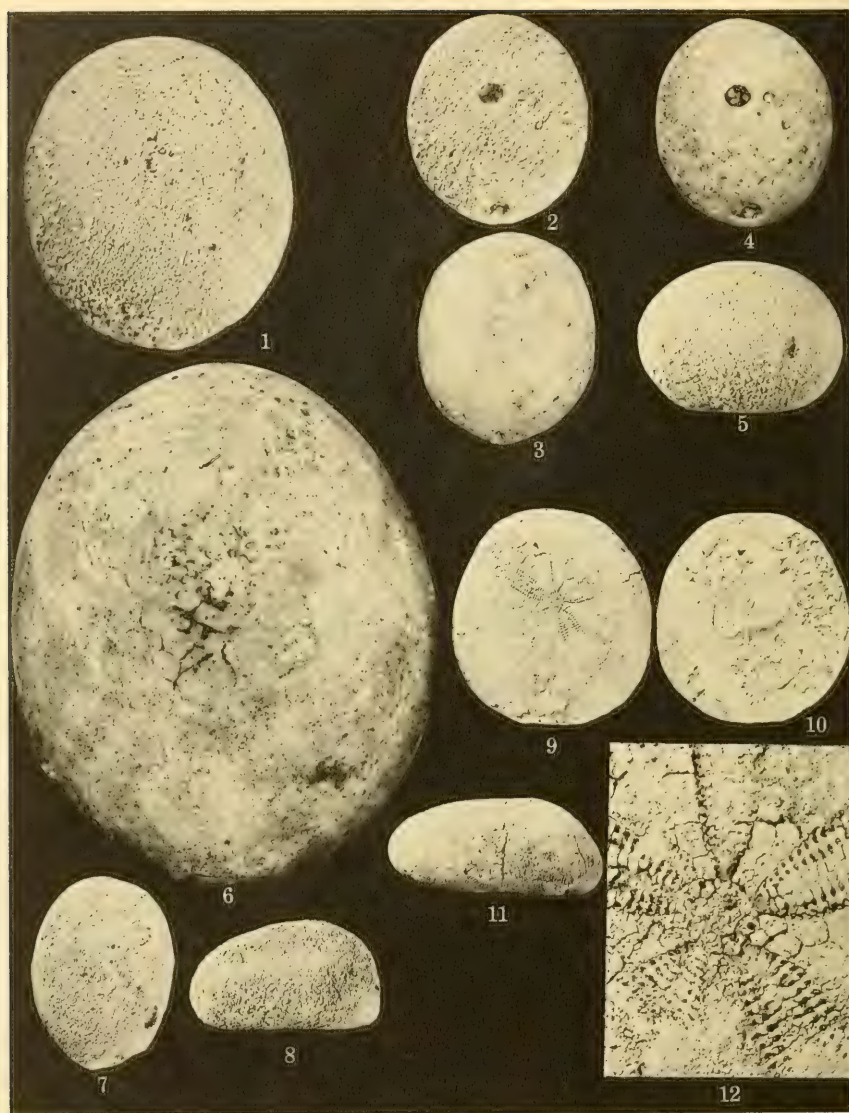




1-4, *PSEUDOPYGAULUS EXCENTRICUS* (DUNCAN AND SLADEN);  
5-8, *PSEUDOPYGAULUS TRIGERI* (COQUAND); 9, 10, *LOVENILAMPAS*  
*BAIXADOLEITENSIS* MAURY

(SEE EXPLANATION OF PLATES AT END OF TEXT.)



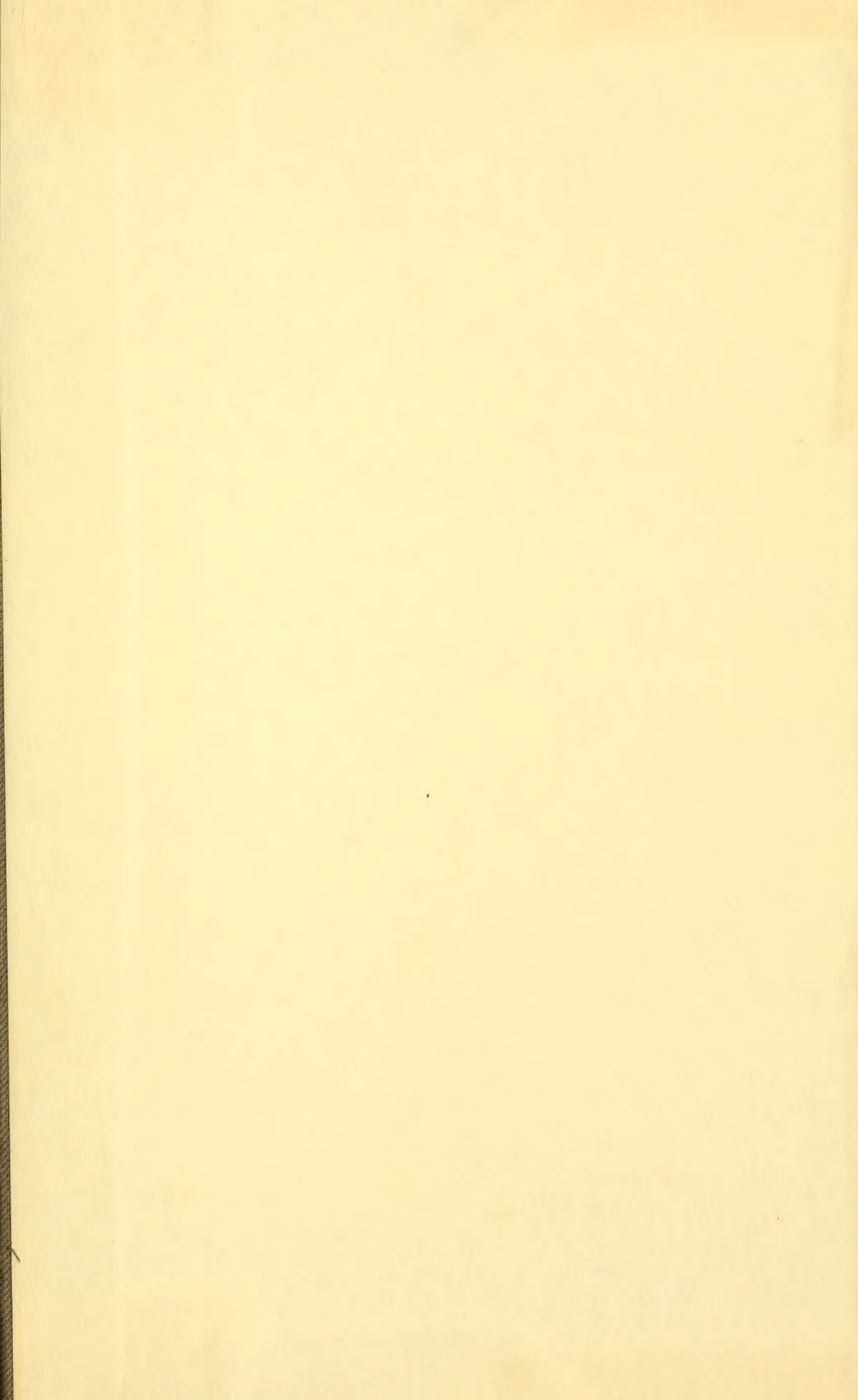


1-5, *OVULECHINUS PILULA* LAMBERT; 6-8, *PSEUDONUCLEUS MALLADAI* LAMBERT; 9-12, *HETERONUCLEUS PERONI* LAMBERT

(SEE EXPLANATION OF PLATES AT END OF TEXT.)









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